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LOCATION OF THE TESTES AND BODY TEMPERATURE IN MAMMALS

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MOORE (1926, 1932) has advanced the hypothesis that the scrotum plays an important rôle in facilitating the maintenance of a temperature optimum for the production of spermatozoa. This hypothesis he has sought to substantiate by evidence of an experimental nature. He has shown in a variety of mammals that if the temperature of the testes is raised a few degrees, either by applying heat to them or by dislocating them into the inguinal canal or body cavity, spermatogenesis is interfered with or finally completely stopped. Recently Moore's observations have been confirmed and extended by the experimental work of Knaus (1932, a, b).

In view of Moore's observations, it lies close at hand to inquire as to whether in mammals there is a correlation between the body temperature of a given species and the fact that the testes may be located either intraabdominally or extraabdominally.

I thought it might be of interest in this connection to collect some of the widely scattered data on mammalian temperatures. It turns out that records for many orders of mammals are either absent or exceedingly fragmentary. Moreover, in view of the fact that some groups of mammals have an exceedingly unstable temperature regulation, the difficulty enters in of properly comparing their temperatures with those of the more stable groups. Some animals are, furthermore, subject to daily rhythms of slight range, whilst others are of wide range, and still others may show no discernible constant daily variation. Moreover, the peak of the daily curve may be diurnal or nocturnal, depending on the waking and sleeping states of the animal. In addition there is a large group of animals in which there are seasonal variations in temperature related apparently to a period of hibernation or torpor. Finally there are mammals which, although they do not hibernate, lead a sluggish existence, which fact may have a bearing upon the body temperature.

A delicate heat regulating center in the brain is believed to have developed in those animals whose body temperature remains fairly constant. Thus mammals

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with little control over heat production and dissipation are thought to be primitive and more reptilian in this regard, whereas those whose control is stabilized are thought to have become more specialized. It will be of interest to see which groups of mammals fall into these two classes.

In spite of the meagreness of the data and the multiplicity of factors involved, it appears possible to arrive at a rough estimate of the prevalent temperatures of quite a number of mammals including some with and some without scrotal testes. The data in the literature are extremely helpful. To these have been added some observations of my own, as well as several sets of unpublished observations for which I am indebted to several of my colleagues, more particularly Drs. R. K. Enders and Frederick A. Gibbs. The temperature readings are expressed in centigrade throughout this paper. Unless otherwise mentioned, the temperatures were obtained by rectum.

OBSERVATIONS

The following groups of mammals have permanently intraabdominal testes:

Monotremata: Echidnidae (spiny ant-eater), Ornithorhynchidae (duck-bill).
Some Insectivora: Centetidae (tenrec), Macroscelididae (African jumping shrew), Chrysochloridae (golden mole).
Xenarthra: Bradypodidae (sloth), Myrmecophagidae (ant-eater), Dasypodidae (armadillo).
Proboscidea (elephant)
Hyracoidea (cony)
Sirenia (sea-cow)
Cetacea (whale)

Of these mammals with permanently intraabdominal testes Weber (1928) sets the Cetacea and Dasypodidae (armadillo) apart by virtue of the fact that he believes they show evidence that the intraabdominal position of the testes is a secondary development, their ancestral forms having been mammals which possessed descended testes. Thus the apparently primitive condition in these animals is to be regarded as a secondary differentiation or reversion.

Of the orders with intraabdominal testes the only ones on which fairly adequate temperature records have been made are the Monotremata and the Xenarthra. Concerning the Proboscidea and the Cetacea there are a few isolated readings, whilst for the remaining orders there are no records. It would be especially interesting to have some observations on the insectivores, with and without descended testes, because they constitute a large and diversified group of extremely primitive mammals. Unfortunately those members of the Insectivora possessing abdominal testes are all tropical forms difficult to procure.

Monotremata

Echidna and *Ornithorhynchus* are believed from numerous considerations to be the most primitive mammals. Records of their body temperatures are fairly numerous. It will suffice for the present purposes to summarize the findings for these animals, quoting the more important papers and indicating the findings briefly.

Echidna:

Average cloacal temperature, 29.4°. Sutherland (1897)
Average cloacal temperature, 31.1°. Wood Jones (1923)
Average summer animals, 30°–32.6°. Wardlaw. Cit. Wood Jones (1923)
Average winter animals, 29.7°–32.3°. Wardlaw. Cit. Wood Jones (1923)
Range of variation 22°–36.6°. Sutherland (1897) (See also Table 1.)

TABLE 1

Range of variation of temperature of Echidna according to Martin (1902)

AIR TEMPERATURE	RECTAL TEMPERATURE	LATITUDE	AIR TEMPERATURE	RECTAL TEMPERATURE	LATITUDE
4	25.5	9.3	5	27.6	12.4
10	27.3		10	30	
20	28.6		20	31.4	
30	30.9		30	33.4	
35	34.8		37	40	

Average temperature 28°–29° with environment at 15°. Martin (1902).

Ornithorhynchus:

Average for *Ornithorhynchus*, 32.2°. Wood Jones (1923)

Average for *Ornithorhynchus*, 30.3°. Burrell (1927) (See also Table 2.)

TABLE 2

Range of variation of temperature of Ornithorhynchus according to Martin (1902)

AIR TEMPERATURE	RECTAL TEMPERATURE	LATITUDE
5	31.8	3.5
10	32	
20	32.6	
32	33.6	
35	35.3	

Average temperature 29°–30° with environment at 15°. Martin (1902).

Monotremes:

Average for, 29.8°.

Air temperature, 15°. Martin (1902)

Xenarthra

To this group belong the sloths (Bradypodidae), ant-eaters (Myrmecophagidae) and armadillos (Dasypodidae), all of which possess undescended testes throughout life. The sloths are characterized by extreme sluggishness, the armadillos are active, burrowing mammals, while the ant-eaters are moderately active. According to Weber the armadillos have testes which are secondarily intraabdominal in that they exhibit anatomical evidence that their ancestors once had descended testes.

Our knowledge of the body temperatures of these groups of animals is recently acquired.

Sloths. Bradypus tridactylus. Ozorio de Almeida and Branca de A. Fialho (1924). 14 observations with external temperature 19°–25.8°:

Maximum rectal temperature..... 32.9
Minimum rectal temperature..... 30
Mean rectal temperature..... 32

Bradypus cuculliger cuculliger. Kredel (1928)

Range 27.7°–36.8°

Air temperature 24.5°–32.4°

Bradypus griseus griseus. F. A. Gibbs.

These observations have never been reported, so they will be given in some detail in Table 3. Two sloths at body temperatures of 33° (26° air temp.) were placed in a cold room and their rectal temperatures read over a period of hours.

TABLE 3

Temperatures of Bradypus griseus griseus

TEMPERATURE OF AIR	RECTAL TEMPERATURE OF		LENGTH OF PERIOD
	Sloth 1	Sloth 2	
26	33	33	0 min.
TEMPERATURE OF COLD ROOM			
14	32	31	12 min.
14	31	31	20 min.
13	30	29	45 min.
13	29	28	1 hr. 15 min.
12	28	27	1 hr. 40 min.
13	25	25	2 hrs. 40 min.
14	24	23	4 hrs. 50 min.
16	24	24	6 hrs. 15 min.
13	24	Animal died	9 hrs. 30 min.
12	23		11 hrs. 55 min.
Animal removed from cold room			
TEMPERATURE OF AIR			
26	23		0 min.
26	24		5 min.
26	26		10 min.
26	26		15 min.
26	27		20 min.
26	28		45 min.
26	29		1 hr. 50 min.

Ant-eaters. *Tamandua tetradactyla.* R. K. Enders
Air temperature, 26.1°.
Rectal temperature, 30°.

Armadillos.

Dasypus (Tatusia) novemcinctus. Ozorio de Almeida and Branca de A. Fialho (1924). 12 observations of rectal temp.: Mean, 34.4°; Max., 35.4°; Min., 33°.

Dasypus novemcinctus. Wislocki

No. 1. Cage temperature, 24°. Rectal temperature, 34.5°, female. Transferred to temperature of 5°.

1 hour at 5°, 33.5
2 hrs. at 5°, 32
3 hrs. at 5°, 31.5
4 hrs. at 5°, 30.5

No. 2. Cage temperature, 28°. Rectal temperature, 35°, male. Transferred to temperature of 0°.

1 hour at 0°, 34
2 hrs. at 0°, 31.5
3 hrs. at 0°, 30

No. 3. Cage temperature, 24°. Rectal temperature, 34.5°, male. Transferred to temperature of 19°.

1 hour at 19°, 33.5
2 hrs. at 19°, 33.5
3 hrs. at 19°, 33
4 hrs. at 19°, 33
5 hrs. at 19°, 32.5

No. 4. Cage temperature, 25°. Rectal temperature, 34.5°, female. Transferred to temperature of 21°.

1 hour at 21°, 33.5
2 hrs. at 21°, 33
3 hrs. at 21°, 32.5
4 hrs. at 21°, 32
5 hrs. at 21°, 31.5
6 hrs. at 21°, 31.5

No. 5. Cage temperature, 24°. Rectal temperature, 33°, male. Transferred to temperature of 11°.

1 hour at 11°, 32.5
2 hrs. at 11°, 31.5
3 hrs. at 11°, 30.5
4 hrs. at 11°, 29.5
5 hrs. at 11°, 29

Transferred to temperature of 21°.

½ hour at 21°, 30.5

No. 6. Cage temperature, 30°. Rectal temperature, 35°, female.

½ hour at 21°, 34.5
1 hour at 15°, 33.5
2 hrs. at 17°, 33
3 hrs. at 18°, 33
4 hrs. at 18°, 32.5
5 hrs. at 19°, 32.5

Brown (1909) gives several figures of temperatures of armadillos without mentioning the atmospheric temperature:

Dasypus sexcinctus, 32.2–34.1; *Dasypus novemcinctus*, 33.1–33.9.

Proboscidea

Records of temperatures on elephants are meagre but the few readings are fairly uniform.

Elephas indicus, old male, 35.7–36.4, Brown (1909)
Elephas indicus, old female, 36.2–36.4. Brown (1909)
Elephas indicus, young female, 35.8–36.6. Brown (1909)
Elephas indicus, 25 yr. old female, 36.2–36.7. Benedict-Fox and Baker Cit. Kanitz (1925)
Elephas oxytis, 15 yr. old male, 35.9. Benedict-Fox and Baker Cit. Kanitz (1925)

Cetacea

The records of whales are practically negligible. The readings are all from stranded individuals and in all likelihood do not represent the normal temperatures of these animals.

Cetacea. 36–37. Cit. Weber (1928)
Orca gladiator. 36.7. Portier. Cit. Kanitz (1925)
Tursiops truncatus. 36. Wislocki

It appears from these data that two groups of animals with undescended testes which have been investigated (the monotremes and the Xenarthra) have relatively low temperatures and extremely unstable heat regulating mechanisms. It is interesting that the heat regulation of the sloth is fully as unstable as that of *Echidna*. The data of Martin indicate that *Ornithorhynchus* possesses more stability than *Echidna*, whilst among the Xenarthra the armadillos appear to be somewhat less labile in their temperature fluctuations than the sloths. In regard to temperature regulation the Xenarthra appear to be fully as primitive as the monotremes.

The fact that these two groups of animals have intraabdominal testes is

somewhat indicative of a possible correlation such as Moore's hypothesis postulates, but is by no means proof of such a contention. The data for the elephant, another form with intraabdominal testes, indicate that this animal's temperature is lower than the average mammalian temperature, but it does not appear to be as low as those of either the monotremes or Xenarthra. Knowledge of the elephant's temperature regulation and its fluctuation applicable to the present discussion must await the accumulation of further observations. The data for cetaceans are also scarcely sufficient to be drawn into the discussion. Knowledge of the insectivores, an important group on which data are completely lacking, would add materially to the subject.

However, some further information may be gained by the reverse procedure, namely an investigation of the temperature of those groups of animals possessing descended testes. In this group the marsupials will be of extreme interest, since they are known to be in many respects primitive mammals, yet have testes which are descended.

TABLE 4

Classification of mammals with descended testes

	SUBINTEGUMENTAL	TRUE SCROTUM	PERMANENT DESCENSUS	PERIODIC DESCENSUS
Marsupialia	Phascolomyidae (wombats)	Majority	All	None
	Notoryctidae (marsupial moles)			
Insectivora	Talpidae (moles)	Tupaiidae (tree-shrews)	Tupaiidae	Talpidae
	Soricidae (shrews)			Soricidae
	Solenodontidae (West Indies)			Solenodontidae
	Erinaceidae (hedge-hogs)			Erinaceidae
Manidae (scaly ant-eaters)	All	None	All	None
Orycteropodidae (aard-varks)	All	None	None	All
Carnivora	Felidae	Majority of Fissipedia	All	None
	Galidictinae (Madagascar)			
	All Pinnepedia (seals, sea-lions, walrus)			
Ungulata	Rhinocerotidae	Majority	All	None
	Hippopotamidae			
	Tapiridae (tapirs)			
Rodentia	Some	Some	None	All
Chiroptera (bats)	None	All	None	All
Lemuroidea	None	All	All	None
Simiae	None	All	All	None

Mammals with descended testes are classified (Weber, 1928) according to whether they possess true scrotal sacs or not, and as to whether they have periodic or permanent descensus of the testes. A preliminary survey has convinced me that there is no clear cut correlation to be obtained, based upon the present data, between temperatures and the presence or absence of true scrotal

sacs (subintegumental or scrotal position of the testes). The question of periodic descensus of the testes will be touched upon later in so far as it applies to the discussion.

The mammals in which descensus of the testes occurs are arranged in Table 4.

Temperature records are lacking on the Manidae and Orycteropodidae, are scant on the Chiroptera and the Insectivora, but fairly abundant on representatives of all the other groups. Concerning one of the insectivores, *Erinaceus* (hedgehog), there are a few data by Pembrey (1903) which can be dismissed in a few words as far as the present discussion goes. *Erinaceus* undergoes hibernation and it was the temperature changes during the period of hibernation and awakening which were being investigated. However, in several animals kept in the laboratory and observed in the waking state during November and December the temperatures recorded next the skin of the abdomen ranged from 32 to 35. No statement is made by Pembrey as to the location of the testes in these animals; normally in the seasonal cycle of *Erinaceus* the testes are retracted into the abdomen by October and hibernation is about to commence. Consequently these temperature readings shed no light for the present purpose upon the relationship of body temperature to testes.

Marsupialia

Numerous observations exist on representatives of this order. No attempt will be made to quote them in detail; instead they will be summarized and the sources in the literature will be given.

Australian Marsupials.

The observations of Martin (1902) given in Table 5 are of considerable interest.

TABLE 5

Temperatures of Australian marsupials (Martin)

	AIR TEMPERATURE	BODY TEMPERATURE	LATITUDE
Dasyurus maculatus (native cat)	5	37.1	2.9
	10	37.1	
	20	36.6	
	30	38	
	35	40	
Bettongia (rat-kangaroo)	5	36.2	2.4
	22	36	
	30	36.2	
	40	38.6	
Trichosurus (Australian opossum)	5	36.1	1.7
	10	36.5	
	20	36.2	
	30	36.2	
	35	37.8	

Average for marsupials, 36.5 with environment at 15 (Martin).

Average 16 species of marsupials, 126 observations, 36, Sutherland (1897).

TABLE 6

Temperatures of Phascolarctos cinereus (koala) (Sutherland)

AIR TEMPERATURE	RECTAL TEMPERATURE
7.7	35
10	35.6
11.5	35.2
13.1	36
16	36.8
19	35.7
22	36
22	36.1
24.5	36.5

Phascolarctos cinereus (koala), 83 observations average 36.4, both sexes; males alone average 35.2 (Sutherland). (See also Table 6.)

Phascolomys lasiorhinus (wombat), 34.3 (single reading)

Phascolomys platyrrhinus, 34

Petaurus (flying squirrel), 5 observations, average 35.7

Dasyurus (native cat), 36 (single reading)

Phalangers (ring-tailed opossum), 22 observations average 36.6 (range 35–37 at 16.8–35 air temperature)

Phalangista vulpina, 36.1
Phalangista fuliginosa, 37.3
Kangaroos:
Macropus giganteus, 36.6 (single reading)
Halmaturus bennettii, 37.1 (single reading)
Petrogale xanthopus, 35.9 (single reading)
Dendrogalus grayi, 37 (single reading)

American Marsupials.

Selenka (1886) mentions that the body temperature of *Didelphys virginiana* is about 36.

Brown (1909) gives several observations placing the temperature of *Didelphys virginiana* between 32.7 and 34.7.

TABLE 7

Rectal temperatures of Didelphys marsupialis (didelphii). Gley and Ozorio de Almeida (1924). Air temperature, 20.2–24.2°

MEAN	MAXIMUM	MINIMUM
34.05	36.2	33
35.96	36.4	34.3
34.70	35.7	31.9

Average 33 observations, 34.6.

Johnson (1931) gives the temperature of an adult male opossum (*Didelphys virginiana?*) as ranging between 36.6 and 35.5 at a room temperature between 25 and 29 (5 observations). The same animal removed to a refrigerator temperature of 4 to 6 degrees showed a range of temperature varying from 33.5 to 34.7.

TABLE 8

Temperatures of Didelphys virginiana (Virginia opossum) (Wislocki)

AIR TEMPERATURE	RECTAL TEMPERATURE
14	32
17	33.5
17	34
18	33.5
20	34.5
23	34
26	33
26	34.5
26	34.5

TABLE 9

Temperatures of Didelphys marsupialis etensis

AIR TEMPERATURE	RECTAL TEMPERATURE	
26.7	34.9	(R. K. Enders)
26.7	34.6	(R. K. Enders)
29	36	(Wislocki)

TABLE 10

Temperatures of Marmosa mexicana isthmica (murine opossum) (Wislocki)

AIR TEMPERATURE	RECTAL TEMPERATURE
21.5	31.5
21.8	31.8
22	30.7
22	31.25
22	31.5
24	33.2
24.5	33.5
24.8	33
25.2	31
29	36
29	36.2

It will be seen from this brief survey that the temperatures of the marsupials are on the average considerably higher than those of the monotremes and the Xenarthra. The data also indicate that the new world Didelphyidae (*Didelphys* and *Marmosa*), considered by all systematists to be the most primitive of recent marsupials, possess lower body temperatures than the marsupials of the old world. The body temperatures of the former (*Didelphys* and *Marmosa*) taken alone do not differ as far as the present data allow one to draw a conclusion from those of the armadillos amongst the Xenarthra. Thus the body temperature of the animals (armadillos) possessing the highest average temperature in the group with abdominal testes is about the same as that of the animals (Didelphyidae) possessing the lowest average temperature amongst the marsupials which have descended testes.

Hence the separation of groups on the basis of temperature in association with descended or undescended testes is not sharp but one of degree only.

The majority of the groups of mammals with descended testes may be dealt with relatively briefly for the present purposes. I present here for a number of groups a summary of data collected by Kanitz (1925) whose work may be consulted for the detailed literature:

Ungulata:
Sheep, 39–40 Minimum-Maximum
Goat, 39–40 Mean
Camel, 34.95–37.85 (A.M.–P.M.)
Pig, 39.5 Mean
Horse, 37.5 Mean
Rodentia:
Rabbit, 38.7–40 Mean
Rabbit, 37.5–41.6 (Air temperature 5–40)
Guinea-pig, 38–39 Mean
Rat { male, 32.1–36.5 (5–40 air temperature)
Rat { female, 33.9–38 (5–40 air temperature)
Coendou villosus, 37.9 mean, 38.3 maximum, 37.3 minimum. Ozorio de Almeida and P. Galvao (1924)

The following data on hibernating rodents are of interest:

Ground-squirrels (*Citellus tridecimlineatus*)

The temperatures of ground-squirrels when not in hibernation according to Johnson (1931) range from about 32 to about 41, but a range of 35–39 is common in a warm room and of 31–36 in a cold room. The lower normal temperatures grade into those of slight torpor at about 29–32.

Prairie-dogs (*Cynomys ludovicianus*)

According to Johnson (1931) 57 daily records on five animals in a warm room showed a relatively stable temperature at 36–37, whereas 46 daily records on seven animals in a cold room ranged between 32 and 36. From these and other observations Johnson concludes that the prairie-dog hibernates only in the coldest weather.

Carnivora:
Dog, 39 Mean
Cat, 39.5 Mean
Cat, 38.5–39.9 (Air temperature 5–40)
Ferret, 39.3 Mean, 37.9–40.4 extremes. Cit. Pembrey (1898)
Fur seal, 38.3 Mean. Hanna (1924)

It may be concluded from these figures that the majority of mammals with descended testes have relatively high body temperatures. Nevertheless amongst those rodents which do not hibernate the rat is conspicuous by possessing an unusually labile temperature. It is also noteworthy that male rats have lower average body temperatures than female rats. The question of sex differences in this regard is one to which relatively little attention has been paid. Sutherland (1897) makes a similar observation concerning the marsupial *Phascolarctos* (koala). He reports the average temperature of eighty-three observations as being 36.4. "However, females at the breeding season are always very decidedly above the ordinary degree of warmth. If such cases be excluded, the average is exactly 36. But the averages for males alone is only 35.2." Moreover according to Bormann, Brunnow and Savary (1923) lower temperatures in males than in females have been reported also for rabbits (Moore) and guinea-pigs (Lipschütz). In their own series of rabbits Bormann, Brunnow and Savary were unable to establish a sex difference in temperature, and they conclude that all previous claims of such differences are open to the criticism of faulty technique. Their argument of faulty technique does not, however, appear to me to explain adequately the fact that it is invariably in the males that the temperature is reported as being lower.

Chiroptera

The writer has had an opportunity to take the rectal temperatures of several tropical bats, which are given in Table 11.

Brief notes exist in the literature to the effect that the temperature of bats which are found in the hibernating state is very low, reaching the level almost of the atmosphere. However, in the non-hibernating season certain bats are reported to have body temperatures as high as 41 or 41.6 degrees (Johnson, 1931).

TABLE 11

Temperatures of bats

	AIR TEMPERATURE	RECTAL TEMPERATURE
Hemiderma perspicillatum aztecum	25.5	37.3
	26	36.4
	28.9	37.8
Phyllostomus hastatus panamensis.	26	37

TABLE 12

Temperatures of Perodicticus potto (Wislocki)

AIR TEMPERATURE MID-DAY	RECTAL TEMPERATURE
27	35.2
28	37.6
29	37.8
30	37
31.5	36.7

Primates

The majority of observations upon the temperature of the Primates are of the Simiae, little account having been taken of the more primitive Prosimiae.

Prosimiae. I had the opportunity on several occasions of taking the rectal temperature of one of the Lorisinae, *Perodicticus potto*, given in Table 12.

The following observations on *Perodicticus potto* are given by Brown: 36.5; 36.2 (3 P.M.); 37.8 (11 P.M.).

For the Galaginae and Lemurinae the following temperatures are cited by Brown:

Galago crassicaudatus..... 37.1
Galago senegalensis..... 38.1
Lemur varius..... 37.7–38.8 (July)
Lemur varius..... 37.9–38 (April)
Galago senegalensis..... 36.2 (3 P.M.)
Galago senegalensis..... 37.8 (3 A.M.)

From composite readings of the temperatures of 22 lemurs, Fox (1923) places their temperatures at 38–39. Their diurnal fluctuations are reported as being irregular.

The Simiae have been the subjects of a number of observations:

Leontocebus geoffroyi, 36.7–40 Fox
Hapale jacchus, 38.8–39.2 2 obs. Brown
Nyctipithecus (Aotus) trivirgatus, 37.4–39.1 2 obs. Brown
Cebus, 37.6–39.1 Fox
Ateles, 37–38.9 Fox
Cercopithecus pygerythrus, 37.8–39.7 Many obs. Brown
Macacus, 37.6–39.1 Fox
Cercocebus, 37.2–39.2 Fox
Cynopithecus, 37.2–38.9 Fox
Papio, 37.6–38.9 Fox
Macacus rhesus, *Macacus rhesus*, *Macacus cynomolgus*, *Papio hamadryas*, *Cercopithecus patas*: Mean rectal, 38. Diurnal range 2–3. Many observations, Simpson and Galbraith (1906)
Macacus rhesus. Mean rectal, 38.2–38.6. Diurnal range, 2–4. Kanitz
Orang utan (*Simia satyrus*), 36.3–37.8 Fox
Chimpanzee (*Pan niger*), 36.3–37.8 Fox
Chimpanzee, 36.8–37.3 Low, high monthly mean during first year of life. Jacobsen, Jacobsen and Yoshioka (1932)
Man, 36.29–37.25 Minimum-Maximum. Diurnal range 1. Benedict and Carpenter. Cit. Kanitz.

It is apparent that the Primates, too, share the relatively high temperatures of the group of mammals with descended testes. It is of interest that the platyrrhine and catarrhine monkeys have on the average higher temperatures than man and that their temperatures are subject to a rather regular diurnal range that is much greater than that of man. Ac-

cording to Fox (1923) the anthropoid apes (orang utan and chimpanzee) have on the whole a mean temperature nearer the human than do the lower monkeys, but they present daily variations far greater than man. The gibbons, to quote the same observer, approach the monkeys in their mean temperatures and daily fluctuations.

The few figures for the Prosimiae indicate that their temperatures are on an average lower than those of the monkeys, approximating the level obtaining in man although there is apparent a tendency for rather wide and irregular fluctuation. No sharp difference is discernible between the body temperatures of the extremely sluggish lorises (*Perodicticus*) and the active Prosimiae (*Galago*, *Lemur*). In respect to sluggishness of life the lorises are comparable to the sloths amongst the Xenarthra and to the koalas amongst the marsupials. The extreme sluggishness of these groups of animals is not apparently linked with a consistently lowered body temperature. The sloths on the one hand have as low body temperatures as any mammal, the koalas and lorises on the other hand have temperatures which approximate fairly closely the temperatures of the more active members of the generic groups to which they belong. It may be, however, that further studies will show that the inactive lorises and koalas possess temperatures of an average level a degree or so below the active members of the groups to which they are related. Of the Australian marsupials, however, Sutherland cites the wombats and the flying-squirrels (*Petaurus*) as having the lowest averages, the sluggish koalas occupying third place.

DISCUSSION

The data presented in this paper do not deny a correlation between body temperature and the location of the testes. Indeed in the main they are favorable to an affirmative answer. Nevertheless it must be borne in mind that our knowledge of mammalian temperatures is on the whole so fragmentary that evidence damaging to such an assumption may arise upon further inquiry. In spite of this scepticism it can be stated that of those mammals with intraabdominal testes which have been fairly adequately investigated (*Echidna*, *Ornithorhynchus*, *Bradypus* and *Dasypus*) the body temperatures are far below the general average for mammals. Contrariwise the mammals with descended testes have, taken as a whole, relatively high body temperatures. The American marsupials exhibit the lowest body temperatures of the entire group with descended testes, their temperatures averaging around 32 to 35. It is difficult to reconcile this low average with Moore's hypothesis. The Australian marsupials, on the other hand, with averages ranging around 36–37 fit well into the group possessing descended testes. Should further data bear out the present indication that the elephant's temperature (undescended testes) is around 36, this would also require explanation to meet the hypothesis.

The occurrence of a periodic descent of the testes in certain hibernating mammals following a rise in body temperature upon awakening and at the onset of the rutting season would appear to be favorable to the hypothesis. According to accounts the body temperatures of hibernating mammals rise rapidly to a relatively constant level within a few hours or days after the termination of the period of dormancy. The body temperatures of those hibernating mammals belonging to the class with descended testes are as high, when not in hibernation, as the temperatures of non-hibernating

mammals with permanently descended testes. According to Johnson (1931), however, the fluctuations may be greater, for he found that the temperature of ground-squirrels when not in hibernation ranged from about 32–41 when subjected to cold and warm rooms. The temperatures of the marmot and woodchuck after awakening are given as around 37 (Dubois, 1896; Rasmussen, 1917). Shortly afterwards the testes descend and the rutting season ensues. In the hedgehog (*Erinaceus europaeus*), according to Marshall (1911), the testes remain descended from April until October coinciding with spermatogenesis and active accessory genital glands. During this period two litters may be born. In the woodchuck, on the other hand, from the account of Rasmussen (1917), the rutting season and the period of spermatogenesis are brief, occurring in April. The testes descend by April, but reascend by July remaining permanently in the abdomen throughout the summer, fall and winter. Excepting for the brief period of rutting, spermatogenesis is practically in abeyance during the remainder of the year. Only one litter is born. Sutherland Simpson (1911–12) took the temperatures of a number of woodchucks captured between July and December and found the temperature range to be between 34.6 and 38.6 with extreme readings from 33.6 to 41.2. Thus in the woodchuck the testes reascend into the abdomen in spite of a continued maintenance of high body temperature. The cessation of spermatogenesis in the re-ascended testes accords well with Moore's view. However, the temperature findings indicate that body temperature is not causally related to the ascent of the testes in this instance. It might be presumed from recent experiments with hormonal extracts that the anterior lobe of the hypophysis plays a significant rôle in the descent and ascent of the testes (Engle, 1932; Moore, 1932, p. 349). Although exposure of the testes to lowered temperature may be necessary for spermatogenesis to occur, the temperature influence is nevertheless only one of a number of factors playing a part in the complex cycle of events underlying periodic descent of the testes. Much more work needs obviously to be done upon the subject of periodic descent of the testes.

Leaving now the question as to whether Moore's hypothesis is borne out by the above findings, several other conclusions are deemed worthy of mention.

1. The lowest average body temperatures recorded in mammals are in *Echidna*. *Ornithorhynchus* and *Bradypus* (sloth) follow in second place with about equal averages and ranges. Next in order are the armadillos and the new world marsupials with approximately equal levels.

2. The new world marsupials (*Didelphys* and *Marmosa*) which have been investigated have a lower average temperature by several degrees than the Australian marsupials. This circumstance may be related to the fact that the new world forms are considered to be the more primitive.

3. A sluggish mode of life is not necessarily associated with a lower body temperature than those of closely related active genera. Three unrelated sluggish groups of animals are the lorises, sloths and Australian koalas. The lorises and koalas do not differ materially in body temperature from the respective groups of active animals to which they belong. The sloths on the other hand have markedly lower temperatures than the related armadillos. If a single reading may be taken as a slight indication, the fairly active ant-eater (*Tamandua*)—rectal temperature 30—shows closer similarity to the sloth than to the armadillo.

4. The Primates present interesting differences in their temperature regulation. The platyrrhine and catarrhine monkeys have higher temperature ranges than man and a greater degree of daily fluctuation. The Prosimiae exhibit a decidedly lower temperature range than the monkeys, but differing from that of man in the wide degree of fluctuation.

LIST OF LITERATURE

BORMANN, F., S. BRUNNOW and E. SAVARY. 1923. Über den Unterschied in der Körpertemperatur beim männlichen und weiblichen Kaninchen und über die Frage der Abhängigkeit der Körpertemperatur von den Geschlechtsdrüsen. *Skand. Arch. f. Physiol.*, vol. 44, pp. 248–261.

BROWN, A. E. 1909. The tuberculin test in monkeys, with notes on the temperature of mammals. *Proc. Zool. Soc. London*, pp. 81–90.

BURRELL, H. 1927. The Platypus. Angus & Robertson, *Sydney*.

DUBOIS, R. 1896. Étude sur le mécanisme de la thermogenèse et du sommeil. Physiol. comparée de la marmotte. *Paris*.

ENGLE, E. T. 1932. Experimentally induced descent of the testis in the macacus monkey by hormones from the anterior pituitary and pregnancy urine. *Endocrin.*, vol. 16, pp. 513–520.

FOX, H. 1923. Diseases in Captive Wild Mammals and Birds. Pp. 520–528, The temperature of monkeys. Lippincott. *Philadelphia*.

GLEY, E., and A. OZORIO DE ALMEIDA. 1924. Température et surface cutanée du bamba (*Didelphis didelphis*). *C. R. Soc. Biol.*, T. 90, pp. 467–470.

HANNA, G. D. 1924. Temperature records of Alaska fur seals. *Amer. Jour. Physiol.*, vol. 68, pp. 52–53.

JACOBSEN, CARLYLE F., M. M. JACOBSEN and J. G. YOSHIOKA. 1932. Development of an infant chimpanzee during her first year. *Comp. Psychol. Monographs*, vol. 9, pp. 1–94.

JOHNSON, G. E. 1931. Hibernation in mammals. QUART. REV. BIOL., vol. 6, pp. 439–461.

KANITZ. 1925. Körper-Temperaturen. *Tabulae Biol.*, vol. 1, pp. 371–391.

KNAUS, H. 1932 a. Die physiologische Bedeutung des Scrotum. *Klin. Wochensch.*, Jahrg. 11, pp. 1897–1900.

———. 1932 b. Zur Physiologie der Spermatozoen. *Arch. f. Gyn.*, vol. 151, pp. 302–329.

KREDEL, F. E. 1928. Note on the temperature of the sloth. *Jour. Mammalogy*, vol. 9, pp. 48–51.

MARSHALL, F. H. A. 1911. The male generative cycle in the hedgehog; with experiments on the functional correlation between the essential and accessory sexual organs. *Jour. Physiol.*, vol. 43, pp. 247–259.

MARTIN, C. J. 1902. Thermal adjustment and respiratory exchange in Monotremes and Marsupials. *Phil. Trans. Roy. Soc. London*, Series B, vol. 195, pp. 1–37.

MOORE, C. R. 1926. The biology of the mammalian testis and scrotum. QUART. REV. BIOL., vol. 1, pp. 4–50.

———. 1932. Sex and Internal Secretions. Edited by Edgar Allen. Chap. VII, Biology of the Testes, pp. 303–354.

OZORIO DE ALMEIDA, A., and BRANCA DE A. FIALHO. 1924. Température et métabolisme du tatou (*Tatusia novemcincta*). *C. R. Soc. Biol.*, vol. 90, pp. 734–735.

———. 1924. Métabolisme, température et quelques autres déterminations physiologiques faites sur le paresseux, *Bradypus tridactylus*. *C. R. Soc. Biol.*, T. 91, pp. 1124–1125.

OZORIO DE ALMEIDA, A., and PAULO GALVAO. 1924. Température et métabolisme de "ourico," *Coendou villosus*. *C. R. Soc. Biol.*, T. 91, p. 1126.

PEMBREY, M. S. 1898. Schäfer's Textbook of Physiology. *London and Edinburgh*, p. 790.

———. 1903. Further observations upon the respiratory exchange and temperature of hibernating mammals. *J. Physiol.*, vol. 29, pp. 194–212.

RASMUSSEN, A. T. 1917. Seasonal changes in the interstitial cells of the testis in the woodchuck (*Marmota monax*). *Amer. Jour. Anat.*, vol. 22, pp. 475–515.

SELENKA, E. 1886. Studien über Entwickelungsgeschichte d. Tniere. Das Opossum (*Didelphys virginiana*). 4tes Heft, p. 106.

SIMPSON, S. 1911–12. Temperature regulation in the woodchuck (*Marmota monax*). *Proc. Amer. Physiol. Soc.*, vol. 29, p. xii.

SIMPSON, S. and J. J. GALBRAITH. 1906. Observations on the normal temperature of the monkey and its diurnal variation; and on the effect of changes in the daily routine on this variation. *Trans. Roy. Soc. Edinburgh*, vol. 45, pt. 1, pp. 65–104.

SUTHERLAND, A. 1897. The temperatures of reptiles, monotremes and marsupials. *Proc. Roy. Soc. of Victoria*, vol. 9 (new series), pp. 57–67.

WEBER, MAX. 1927. Die Säugetiere. *Jena*.

WOOD JONES, F. 1923. The Mammals of South Australia. Part 1.

SOME PROBLEMS OF THE ORIGIN, CIRCULATION AND ABSORPTION OF THE CEREBROSPINAL FLUID

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SINCE the discovery of cerebrospinal fluid in 1774 by Cotugno, a great amount of work has been directed to an understanding of the fluid. Yet many of its most elementary problems still receive dissenting answers and agreement today often exists only within the school of a particular investigator. Identical methods have frequently yielded various results and equivalent results have received diverse interpretations. A review must in consequence consider many points of view and risk being laborious and hypercritical in its effort to evaluate the worth of existing data.

This review is concerned largely with work done on the cerebrospinal fluid during the past ten years. Investigations of an earlier date have been discussed by Weed (1922). We shall consider here the sites of origin and escape of the fluid, its circulation and the so-called mes-ectodermal barrier between it and the blood. For discussions of the pressure of the cerebrospinal fluid, see the reviews by Weed (1922 and 1933).

THE SOURCES OF THE CEREBROSPINAL FLUID

Intraventricular Source

The occurrence of an internal hydrocephalus after obstruction of the aqueduct of Sylvius by pathological processes or experimental means has provided unequivocal evidence of an intraventricular source of cerebrospinal fluid. Investigation has been directed toward measuring the part played by the chorioid plexuses and the ventricular ependyma with the result that three views have been formulated: first, that the plexuses account for the major portion of the fluid and the ependyma only a relatively small increment; second, that the plexuses take no part in its production; third, that the ependymal cells are not concerned with fluid-formation.

Histological studies first directed attention towards the high columnar epithelial cells of the chorioid plexuses as a source of cerebrospinal fluid. Intracellular globules and granules were described and an attempt was made to correlate their relations with secretory activity. After critically reviewing the results of these investigations, Weed (1922), came to the conclusion that "there is no conclusive evidence that these intracellular structures constitute the intracellular mechanism for the elaboration of cerebrospinal fluid. The difficulty of final demonstration that these granules are discharged into the fluid or are in some way dissolved in that fluid, cannot at present be surmounted."

The last ten years have been without evidence which in any way weakens this conclusion. More recently Davis (1923–24) has studied the granules of the epithelial cells; on the basis of their reactions to fixatives and to stains, he decided that they are mitochondrial in nature and without a secretory rôle. It is consequently justifiable to state that histological studies

on the normal epithelial cells of the chorioid plexus have provided no evidence that these cells are concerned in the production of cerebrospinal fluid.

Evidence more difficult of evaluation has come from study of the chorioid plexus after administration of drugs and hypotonic solutions. It has long been known that, among other drugs, pilocarpine, ether and theobromine cause a striking increase in volume of the epithelial cells of the plexus. These elements double in height, most of the volume-increase coming from enlargement of the clear, vesicular, apical portion. Changes of the same sort, often to an even greater degree, have been reported by Weed (1923) following intravenous injections of hypotonic solutions. In these experiments with distilled water, the great increase of cell-size led to bulging, sometimes apparently to rupture, of the limiting membrane. There is no question, therefore, that hypotonic solutions and certain drugs lead to profound morphologic changes in the epithelial cells of the chorioid plexus.

Can these changes be accepted as evidence that the epithelial cells are concerned in the formation of cerebrospinal fluid? It has been thought, on the basis of inadequate and possibly misleading evidence (see Becht and Gunnar, 1921) that increase of cell-size is accompanied by an increased escape of fluid from the plexuses. Analyzing the morphologic changes produced by drugs, Becht (1920) contrasted the plexus cells with those of a typical gland such as the parotid. In the latter, increased activity is evidenced by reduction in size of the alveoli and the appearance of a clear zone at the base of the cells; in the former, supposedly increased activity is accompanied by increased size of the plexus cells which have a clear zone at their free ends. The implied criticism assumes an identity of secretion-processes in all types of gland-cells and because of the varied histological appearances of secretory activity cannot be relied upon. If it be agreed with Weed (1923), that the increased cell-size after intravenous hypotonic solutions is simply due to an intracellular accumulation of water and that the associated increase in cerebrospinal fluid pressure may be completely explained by an increase in brain-volume and intracranial blood-volume, we are again without evidence of new formation of cerebrospinal fluid. The data simply indicate that more fluid enters than leaves the cells without in any way demonstrating that fluid actually escapes from unruptured cells into the ventricle. The change is probably produced by passage of fluid from a medium of low osmotic pressure, the blood, to one of higher osmotic pressure, the epithelial cell. Here, then, are important observations which must at present go without final explanation. Accurate measurement of the rate of cerebrospinal fluid-formation with control of vascular reactions will aid greatly in an understanding of the cellular changes just discussed.

Certain observations have been made directly on the chorioid plexuses. Cushing (1914) reported that he saw fluid exuding from the plexus of a lateral ventricle in man; Howe (1929) made similar observations on experimental animals. Schaltenbrand and Putnam (1927) injected fluorescine intravenously, observed the plexus of the living animal with a microscope, and saw greenish fluid coming from the surface of the plexus. These results are all faced with the same objections—the plexus has in each instance been exposed to air and subjected to a pressure much below normal. That the arachnoid membrane "sweats" fluid under similar conditions is a rather common observation, but this is urged by no one as evidence of normal function.

In their important reports on experimental hydrocephalus, Dandy and Blackfan (1914) and Dandy (1919) offered evidence which seemed to them to be direct and conclusive. Because their results have been practically universally accepted as decisive, it is perhaps justifiable to discuss them in some detail.

Dandy (1919) described a unilateral hydrocephalus in dogs produced by occluding one foramen of Monro. He also found that if the foramen was blocked and the chorioid plexus removed at the same time, a collapsed ventricle resulted. As far as can be ascertained from the article, though a direct statement is lacking, this last kind of experiment was successful on only two animals. It was concluded that the plexus alone is responsible for the formation of cerebrospinal fluid.

In Dandy's experimental procedure, the foramina of Monro were plugged and the chorioid plexus removed through transcortical incisions. It is quite obvious that such an operation, even in the most skilful hands, is delicate and difficult, and calls for clear demonstration that its aims have been fully realized. It must first have been certain, at the end of the experiment that the foramina of Monro were so completely blocked as to make escape of fluid impossible. Dandy apparently relied solely on macroscopic inspection, since no mention was made of microscopic examination or demonstration (for example, with a colored solution) that the block between the ventricles was complete. The dilatation of the ventricle with intact plexus is not to be regarded as an adequate control. There was the further necessity of demonstrating microscopically that there was no possible escape of fluid through the healed transcortical incision from the ventricle directly into the subarachnoid space; figure 7 of the 1919 communication indicates that this was not altogether improbable. And this demonstration must include evidence that the ventricular ependyma at the site of the wound was intact; otherwise fluid might well have passed from the ventricle into the substance of the brain. Any one of these three objections, if valid, would appear to impair the conclusions drawn from the experiment.

It is rather difficult, moreover, to be certain that the chorioid plexus was completely removed from the lateral ventricle. Describing the operation in which the aqueduct of Sylvius was occluded and the chorioid plexuses of both lateral ventricles extirpated, Dandy and Blackfan (1914) stated: ". . . . a good exposure of the entire lateral ventricle was obtained and the choroid plexus almost completely extirpated." Again: "An internal hydrocephalus had resulted from the occlusion placed in the aqueduct of Sylvius thirty-five days previously, *in spite of the almost complete bilateral extirpation of the choroid plexuses of the lateral ventricles.*" The italics are those of Dandy and Blackfan. Five years later, describing the same experiment (this is evident from the illustrations), Dandy (1919) stated: " . . . . the choroid plexus of both lateral ventricles was removed. . . . . The accumulated cerebrospinal fluid forms *solely* from the choroid plexus of the third ventricle." Here, then, is a discrepancy which may be important. Description of an experiment in 1914 states that the plexus was *almost* completely extirpated; in 1919 it is to be inferred that in the same experiment, and in others involving the same operative procedures, plexectomy was *complete*. Though Dandy's work may be fully substantiated in the future, at present his conclusions appear acceptable only with reservations.

Some collateral but not direct evidence suggesting that the chorioid plexus is con-

cerned in the formation of cerebrospinal fluid has come from embryological studies. Weed (1917), in embryo pigs, noted that the first extraventricular spread of cerebrospinal fluid is correlated with beginning tufting of the plexus. The same picture was found in *Amblystoma punctatum* by Flexner (1929). He also noted that in every instance brain transplanted from several of these embryos to the brachial or flank region of other *Amblystoma* developed chorioid plexuses and ventricles which were sealed off at their ends. After about two months in the hosts, several of these transplants were distended into great, thin-walled cysts filled with fluid. Similar transplants of spinal cord, in which fluid-formation would have to occur without chorioid plexus, were never dilated to this degree. These findings are offered simply as suggestive evidence that the plexus is in some way responsible for production of cerebrospinal fluid.

Relatively few investigators have dissented from the opinion that the plexuses have to do with fluid-formation. Among those disagreeing is Coupin (1930) who reported studies on fish. He pointed out that the meningeal space in ganoids and cyclostomes lacks fluid but instead is filled with adipose or myxomatous tissue. Chorioid plexuses, however, are present and particularly well developed in the cyclostomes. The apparently complete absence of cerebrospinal fluid in the presence of apparently well-developed plexuses led Coupin to the general conclusion that the two are in no way related—certainly an assumption not to be carried to other animal forms without many reservations. He is in part answered by Kappers (1926), who found that fluid is lacking in the leptomeningeal spaces, but that there is good evidence of its presence within the ventricles. All these investigations on fish have been made on fixed material in which the demonstration of cerebrospinal fluid is uncertain, perhaps impossible. It is not yet finally determined, therefore, whether extraventricular fluid is lacking in ganoids and cyclostomes. The "meningeal space" filled with adipose or myxomatous tissue may be homologous with the epidural space of mammals which also contains adipose tissue. If this be true, the "meningeal space" of fish should not be confused with the subarachnoid space of mammals.

Having noted in cases of ventricular hemorrhage that the epithelial cells of the chorioid plexus contained hemosiderin granules, Askanazy (1914) suggested that the plexus might be concerned in the absorption of cerebrospinal fluid. Hassin, Isaacs and Cottle (1922) and Wüllenweber (1924), corroborating these findings, stated that they are to be taken as definite evidence of absorption by the plexus. Klestadt (1915) injected carmine, fat and glycogen into the ventricle, found them all in the epithelial cells of the plexus, and so concluded that cerebrospinal fluid was being absorbed. These views, very briefly outlined here, find their extreme expression in Hassin (1930a and several other papers) who, on the basis of these observations and highly questionable pathological findings, concluded that the chorioid plexus absorbs certain constituents of the cerebrospinal fluid and assumed that it is not concerned with its formation. It seems highly probable that these conclusions are unwarranted, that the observations mentioned are not associated with absorption of cerebrospinal fluid but are to be related to phagocytosis and to the same sort of cellular activity which accounts for the storage of vital dyes.

The contribution made by the ependymal cells to the ventricular fluid is difficult to measure and few data have been offered to a solution of the problem. On

the basis of the experiments discussed above, Dandy (1919) concluded that the ependyma takes no part in its formation. Wislocki and Putnam (1924) sacrificed animals about an hour after intravenous injection of potassium ferrocyanide and iron ammonium citrate; after proper fixation, Prussian Blue granules were found in the ependymal cells of the areae postremae at the caudal end of the fourth ventricle. It was consequently suggested that the ependymal cells of these areae made a small addition to the ventricular fluid. Weed (1917), finding evidences of fluid in the ventricles of pig and human embryos before the appearance of the chorioid plexus, concluded that in embryos at least the ependymal cells take part in fluid production. Corroboratory evidence was found in transplants of the spinal cord of *Amblystoma* by Flexner (1929). In some of these transplants the central canal was small, but in others high, columnar ependyma was correlated with formation of fluid-cavities about as large as the fourth ventricle of the normal embryo. Finally, by microscopic examinations done in much the same way as those on the living chorioid plexus, Magnus and Jacobi (1925) found evidence of fluid coming from the ependymal cells.

It is evident from the foregoing discussion that we lack exact evidence of the sources of the intraventricular fluid. No experiment has as yet been devised to give an unequivocal answer to the problem. Despite the weakness of our data, however, it is probably justifiable to work with the hypothesis that the chorioid plexuses make the major contribution to the fluid. Their high vascularity, great surface area and the weight of experimental evidence speak in favor of this assumption. In the same unsatisfactory way, it is to be supposed that the ependyma adds a relatively small amount of fluid to that elaborated by the plexus. Our foundation for quantitative statements is so inadequate, however, that it would furnish little challenge to valid contradictory observations.

Extraventricular Sources

The history of the development of our present views on the histology and physiology of the perivascular spaces of the central nervous system has recently been presented by Schaltenbrand and Bailey (1928). The very brief account to be given here of the opinions of early investigators is taken almost entirely from their article.

The spaces about the blood vessels of the brain were first described by Pestalozzi (1849). Subsequently Virchow (1851), Robin (1859), His (1865) and Roth (1869) made contributions to the subject but the first description agreeing fairly closely with that now rather generally accepted came from Key and Retzius (1876). These last investigators believed that the blood vessels, piercing the leptomeninges and subarachnoid space to dip into the brain, carried with them a visceral endothelial cellular layer corresponding to the arachnoid membrane and a parietal layer of endothelial cells corresponding to the pia mater. The space between these two layers of endothelial cells was designated the perivascular space. The processes of glial cells were said to be in intimate connection with the cerebral side of the vascular pia. The parietal wall of the perivascular space might consequently be looked upon as a pial-glial membrane. Held (1909) largely agreed with this view and it has since been accepted in its essentials by Cushing (1925), Weed (1914) and others. Spielmeyer (1922), however, has questioned the conclusion that the perivascular spaces constitute true fluid-channels in the brain and is of the opinion that only indeterminate spaces are present

within the loose tissue of the adventitia of the blood vessels.

The problem has more recently been reinvestigated by Schaltenbrand and Bailey (1928). They concluded that the perivascular spaces around the larger vessels are bounded by two connective tissue layers corresponding to the pia and arachnoid or lie in a loose connective tissue of leptomeningeal origin and not to be split into layers. This is a view very similar to that of Key and Retzius. The tissue about the smaller vessels is said to be derived from the pia and lies either apposed to the muscularis or the endothelium of the vessel.

Several investigators (see Essick, 1920), using a method of silver staining, have found in the central nervous system the same picture of fluid-spaces lined by mesothelial cells as originally given by Key and Retzius. Schaltenbrand and Bailey, however, were unable with silver stains to demonstrate except rarely a layer of endothelial-like cells either in the subarachnoid or perivascular spaces. All the cells seen in their preparations gave rise to fibers, though the fibroblasts of the pia next to the spaces were often found to be somewhat flattened. They consequently inferred that the leptomeninges are without a layer of endothelial cells. An equivalent observation was made by Mallory (1920) in the subarachnoid space. Vital staining of the meninges, in the hands of Woollard (1924) and Kubie and Schultz (1925) has led to the identification of arachnoid lining cells thought to be truly mesothelial and so distinct from fibroblasts. The irregularity of results obtained with the silver technique might consequently be considered unimportant in view of the findings with the method of vital staining. Those investigators who have failed to find mesothelium lining the subarachnoid or perivascular spaces have been so positive in their identification of fibroblasts, however, and the nature of the cell-type lining these fluid-spaces is so important to an understanding of the permeability of the lepto-meninges, that it seems well to leave the question open for future work. It seems proper, nevertheless, to add that the weight of evidence favors the view that mesothelial cells line the extraventricular pathways of the cerebrospinal fluid.

The cerebral side of the pia was found closely opposed to a glial membrane, the Limitans glia, by Schaltenbrand and Bailey. Astrocytes were seen to send their foot-plates down to the pial membrane in such a way that in all vessels, except possibly capillaries, glia and pia together formed an uninterrupted membrane. His' space, thought to lie between glial and pial cells, was consequently judged to be an artifact.

His in 1865 was the first to demonstrate those spaces about the nerve cells of the brain called pericellular or perineuronal spaces. Mott (1910) made an important contribution while studying experimental cerebral anemia when he found that these spaces open into the perivascular spaces. Evidence in substantiation of Mott's pathway came from Goldmann's (1913) injection of spaces about the ganglion cells with trypan blue introduced into the subarachnoid space. Using a moderately elevated pressure in the subarachnoid space, or after cerebral anemia caused by ligation of the arteries in the neck, Weed (1914) was also able to inject the perineuronal spaces via the perivascular spaces with the Prussian blue reagents. Weed followed Prussian blue granules through pericapillary spaces. A leptomeningeal sheath was also seen by Schaltenbrand and Bailey about the capillaries, but, unlike the larger vessels, there was no lumen between the sheath and the vessel wall.

The experiments of Mott on cerebral anemia led him to the view that cerebrospinal fluid flows normally from the subarachnoid spaces through the perivascular spaces to the pericapillary or perivenular spaces. This is a view which today has been abandoned. The old experiments of Spina (1899) in which drops of fluid were seen on the surface of a brain prolapsed after production of an experimental hypertension are against this view. Recently Magnus and Jacobi (1925), observing the surface of the brain with a microscope, obtained much the same results as gotten by Spina. The most significant evidence against Mott's view, however, has been given by Weed (1914). He irrigated the subarachnoid space for several hours at normal pressures with the Prussian blue reagents and failed to find the reagents in the perivascular spaces. He concluded, therefore, that flow in these spaces is seemingly towards, not away from, the subarachnoid space.

It appears probable, then, on the basis of the best available observations, that there is a remarkably definitive fluid-pathway from the neurones to the subarachnoid space. Around each neurone, in the present view, is a minute or "potential" perineuronal space, probably equivalent to the tissue spaces of other organs, which communicates with the loose connective tissue around a capillary. The pericapillary tissue in turn leads into the larger perivascular space. The visceral wall of this space is formed by cells carried down from the arachnoid membrane. The parietal wall is composed of pial cells and the prolongations of astrocytes in intimate connection with the fibroblasts of the pia. Doubt exists as to whether the space is lined by an endothelium or mesothelium or by slightly differentiated fibroblasts.

One more important question remains to be discussed. Is it possible to gain a measure of the amount of fluid flowing from the perivascular spaces to the subarachnoid space? In a review, Weed (1922) concluded that "the perivascular spaces . . . . pour a certain amount of fluid into the subarachnoid space, where this fluid mixes with the liquid produced in the cerebral ventricles." As is also noted by Weed (1914), "the space about the nerve cells is probably chiefly potential in character, filled during life by a very thin layer of fluid." Schaltenbrand (1928) has concluded that a stream of cerebrospinal fluid from the perivascular spaces to the subarachnoid space is not definitely disproved but appears to be unlikely. This opinion is based on evidence from two sources. Having injected fluorescine intravenously, Schaltenbrand and Putnam (1927) observed the surface of the brain of the living animal with a microscope and failed to see any escape of dye such as might be anticipated were there fluid flowing from the perivascular spaces. In their histological studies on normal brains, Schaltenbrand and Bailey (1928) noted the absence of a true space about the capillaries and smaller vessels. In another effort to test the view that there is a fluid-stream from the perivascular spaces, these investigators studied the size of the spaces after disease or experimental procedure had supposedly occluded the subarachnoid space. The finding of spaces of apparently normal size in such cases appeared to them to substantiate the conclusion that a circulation of perivascular fluid under normal conditions is improbable. As far as can be judged from the description of their experiments, however, there is no clear evidence that they were dealing with complete occlusion of a part of the subarachnoid space.

As will be discussed later in considering the circulation of the cerebrospinal fluid, the amount of fluid flowing from the

ventricles is small. In the cat it appears that only about 0.6 cc. per hour flows into the subarachnoid space from the ventricles. In view of their great numbers, it is apparent that all the perivascular spaces may make a small but significant contribution to the fluid in the subarachnoid space though the amount of fluid leaving any particular space be minute. The evidence at hand does not appear to controvert this view. The perivascular spaces, as will be discussed later, are perhaps best to be regarded as an accessory pathway for drainage of the tissue-fluid of the central nervous system. They are in this sense analogous to the lymphatics of other organs. If drainage from them be interrupted, as for example may happen in experimental occlusion of the subarachnoid space, compensation may be anticipated through increased absorption by the venules. The lack of a true space in the loose tissue around the capillaries and smaller blood vessels, and the presence of a true space filled with fluid around the larger vessels, is compatible with the view that the capacity about a stem-vessel must be large in order to receive the very small amounts of fluid present about each of its many branches.

It appears certain that under normal conditions no more than very small amounts of fluid pass into the subarachnoid space from a single perivascular space. The evidence at hand makes it difficult to add any exactness to this very unsatisfactory statement. It may be added, however, that it is not unreasonable to suppose that normally there is a very sluggish, probably irregular or interrupted, movement of fluid from the perivascular spaces to the subarachnoid space. The presence of fluid in the spaces about the larger vessels speaks in favor of this opinion. So too do the observations of Kubie and Schultz (1925). Having given hypotonic solutions intravenously, they found evidence of a definitive fluid-stream in the perivascular spaces, leucocytes lying in these spaces being "washed out" into the subarachnoid space. It appears reasonable, therefore, to assume that by decreasing the osmotic pressure of the blood, they simply magnified a very slow movement of fluid which normally takes place.

That certain of the constituents of the cerebrospinal fluid vary in their concentrations at different levels of the central nervous system is well established. The protein of the fluid, for example, increases in concentration from the ventricles to the lowest portions of the subarachnoid space whereas the glucose is in slightly greater concentration within the ventricles. This variation in concentration has been explained by some on the basis of admixture of perivascular fluid, relatively rich in protein and poor in sugar, with fluid from the ventricles and has been given as suggestive evidence of flow from the perivascular spaces. Other explanations, perhaps less satisfactory, suggest themselves for these findings. It is possible that the water of the cerebrospinal fluid is more rapidly absorbed than is the protein and that consequently fluid furthest removed from its source is richest in protein. A diminution in the concentration of sugar may perhaps be due to its use by the cells lining the subarachnoid space. The supposition is made by some that these differences in chemical constitution arise because of admixture of fluid which seeps through the walls of the blood vessels traversing the subarachnoid space.

There is a little evidence suggesting that cerebrospinal fluid arises from the blood vessels within the subarachnoid space. After intravenous injections of urea and sodium salicylate, Cestan, Laborde and Riser (1925) found equivalent concentrations of these substances at different levels

of the subarachnoid space after about twenty minutes. The same results were obtained after isolating the lower subarachnoid space from the ventricles by ligature. The permeability of the vessels of the subarachnoid space to the dye fluorescine has also been studied. After injecting it intravenously, Schaltenbrand and Putnam (1927) observed that it escaped first from the arteries into the cerebrospinal fluid and a short time later, in smaller concentration, from the veins. In their discussion of the extraventricular sources of cerebrospinal fluid, Schaltenbrand and Bailey (1928) concluded from these results that the vessels of the subarachnoid space must be considered as sources of the fluid.

In studies on vascular permeability in skeletal muscle, Rous, Gilding and Smith (1930) failed to find any vessels larger than fine arterioles and venules permeable to their large series of dyes. Much the same condition with respect to qualitative correlation of vessel size and permeability exists in the skin (Smith and Rous, 1931). As far as is known, though the published data are old and in many ways inadequate (Adamkiewicz, 1882; Kadyi, 1889; Poirier and Charpy, 1892–1902), the vessels of the subarachnoid space are arteries and veins and there are no arterioles, venules or capillaries present. Experience in other regions of the body, therefore, indicates that vessel-permeability in the subarachnoid space is probably insignificant.

Moreover, to conclude from experiments with a single dye that the vessels of the subarachnoid space contribute to the cerebrospinal fluid appears to be dangerous. As pointed out by Rous and his coworkers (1930), comparison of the results gotten with a series of dyes should be made to rule out possible toxic effects of a single dye. Care must also be taken to avoid even slight injury to vessels or changes in temperature or intensity of light, otherwise vessel permeability may be significantly increased (Hudack and McMaster, 1931, 1932). The rate of escape of dyes from vessels can be taken as only a crude index of the normal rate of escape of substances from the blood; in the case of the dyes, escape is much accelerated by a concentration gradient which does not exist for normal substances. The results of Schaltenbrand and Putnam, therefore, are to be considered only suggestive. Final interpretation awaits experience with a large number of substances under carefully controlled experimental conditions. The results which appear most significant in indicating a permeability of the vessels of the subarachnoid space important for the composition and perhaps the quantity of cerebrospinal fluid are those of Cestan and his coworkers.

The data at hand appear to indicate that the amount of fluid arising outside of the ventricles is very small—very much less than that originating within the ventricles. This conclusion is in agreement with the investigations of Riser and Sorel (1928) who attempted to measure, with quite uncertain methods, the amount of cerebrospinal fluid formed within the subarachnoid space. There is a little evidence, far from conclusive, which indicates that small quantities of cerebrospinal fluid may originate from the vessels of the subarachnoid space. It appears more likely, however, that fluid of extra-ventricular origin comes from a sluggish, irregular movement of small amounts of perivascular fluid into the subarachnoid space.

THE ABSORPTION OF THE CEREBROSPINAL FLUID

The Venous Sinuses of the Cranial Dura Mater

In his review of the cerebrospinal fluid Weed (1922) has discussed comprehensively the evidence indicating a major

absorption of cerebrospinal fluid into the large venous sinuses of the cranial dura mater. The background for this view has come from various physiological and anatomical observations. Foreign solutions injected into the subarachnoid space of living animals have been detected in the blood in less than a minute, but appear in the lymphatics only after much time and then in low concentrations. It has consequently been argued that cerebrospinal fluid drains in major part into the venous system. Key and Retzius (1876) and other of the early investigators concluded that passage of fluid from the subarachnoid space into the venous system took place via the Pacchionian granulations of the large cranial dural sinuses. Subsequent research, however, failed to demonstrate these granulations in infants and certain experimental animals, and they were therefore discarded in accepted explanations of the absorption of cerebrospinal fluid.

The problem remained without important contributions until the work of Weed (1914). He examined microscopically the cranial dural sinuses of animals and infants and found in them all so-called arachnoid villi. These villi, in his description, have a cylindrical base of myxomatous tissue lying in a frame-work of fine, reticular connective tissue. The myxomatous basilar structure is capped on all sides by mesothelial arachnoid cells. Many of the villi surround small cerebral veins emptying into the dural sinuses. And, most important, the villi invade the dural walls of the venous sinuses or their lateral lacunae so that the caps of arachnoid cells come in contact with the endothelium of the sinuses. The Pacchionian granulations are considered to be old, hypertrophied villi.

The pathway by which a foreign solution escapes from the subarachnoid space was next studied by Weed with the use of isotonic potassium ferrocyanide and iron ammonium citrate. After irrigating the subarachnoid space with this solution under normal pressure for three or four hours, the animal was killed and promptly fixed with acid formalin. Under these conditions, Prussian Blue granules were precipitated wherever the reagents had been present. Microscopic examination of the material then demonstrated granules of Prussian Blue within the mesothelial cells covering the villi, the endothelial cells lining the venous sinuses and the sinuses themselves. It was consequently concluded by Weed that cerebrospinal fluid escapes from the subarachnoid space into the cranial dural sinuses by way of the arachnoid villi.

This concept is today widely accepted. Halliburton (1916), Cushing (1925), Winkelman and Fay (1930) and many others have adopted it in practically all its particulars. The observations of Le Gros Clark (1920–21) and Winkelman and Fay (1930) on the distribution of the villi and Pacchionian granulations substantiate those of Weed. These structures have been found projecting not only into the sinuses proper but more frequently into the lacunae laterales communicating with the sinuses and formed by terminal arborizations of the cerebral and meningeal veins. Winkelman and Fay at no time found blood in these lacunae and regard them as being filled during life with cerebrospinal fluid. To reiterate, then, cerebrospinal fluid flows from the subarachnoid space through arachnoid villi and Pacchionian granulations into the lateral lacunae and thence into the large sinuses with which these lacunae directly communicate.

Several investigators have expressed doubt that the pathway just described is of importance in the absorption of cerebrospinal fluid. Their criticisms, however,

appear to lack finality. Papilian and Jippa (1925) without valid experimental evidence concluded that this mechanism has no appreciable rôle in the circulation of cerebrospinal fluid. Howe (1929) contended that this explanation is inadequate and that were it correct, fluid must enter the subdural space and subsequently pass through the dura into the venous sinuses. His criticism was apparently made without consideration of the observations showing that the subdural space is obliterated (Weed, 1914; Le Gros Clark, 1920–21) at the point where the villi penetrate the dura and approach its sinuses and that the dura is either a relatively very thin membrane or actually absent over the villi. His suggestion that the villi may be concerned in the entrance of subdural fluid, however, merits investigation.

A new approach to the problem has recently been attempted by Dandy (1929). He reported separation of the brain, with the arachnoid and pia presumably intact, from the longitudinal, circular and transverse sinuses of young dogs. The animals are reported to have been without distress at all times and to have had no evidence of hydrocephalus from four to six months after the operation. Dandy accepts these findings as conclusive evidence that the arachnoid villi are not normally concerned with the absorption of cerebrospinal fluid but that it drains directly into the blood vessels of the subarachnoid space. This conclusion appears doubtful in the light of several objections. Villi have been described by Elman (1923) as being present in the spinal arachnoid membrane. There exist, therefore, mechanisms perhaps like those presumably destroyed by Dandy which may assume the function of the lost villi and prevent abnormally large accumulations of fluid in the cerebrospinal fluid pathways. There appears to be some reason to anticipate this compensation: reduction in the size of the absorbing surface must lead to relatively small increases of cerebrospinal fluid pressure; this pressure-increase causes an increased absorption rate through the intact villi so that accumulations of fluid detectable as hydrocephalus may well be absent. There is a further objection to Dandy's experiments. The statement that all the villi were separated from the sinuses—a difficult operative feat—and the implication that they were without contact with the dural sinuses for six months after the preliminary operation calls for microscopic confirmation. Without this, the possibility of incomplete separation and of villus regeneration, a wholly unexplored problem, cannot be excluded.

It appears justifiable, consequently, to state that the interpretations of Weed are without valid experimental contradiction. The method of determining the normal routes of fluid-flow by means of foreign solutions, the whole basis of the theory, requires, however, most careful and cautious scrutiny before it is to be judged acceptable. Weed himself has been painstaking in his use of the technique. After death, animals were quickly fixed with the precipitating acid-formalin solution. Experiments in which there was diffuse staining of the leptomeninges were discarded as unsatisfactory. There is the possibility, not to be defined quantitatively however, that post-mortem diffusion patterns might have given a picture inaccurate for the living animal. This criticism has its foundation in the thought that the actual time necessary for complete precipitation of the Prussian Blue in the subarachnoid space might have been longer than the apparent time necessary for so-called complete fixation of the tissues. It might be assumed, consequently, that due to a differentiation of the cells of the arachnoid villus, peculiar diffusion

patterns occur within them which lead to the same sort of artifact which long confused the physiology of the kidney. Justification of the method in answer to this criticism is to be found in the failure to detect Prussian Blue granules in the blood vessels traversing the subarachnoid space, in the meningeal vessels, or in the perivascular spaces—the only evident pathways besides the villi from the subarachnoid space to the blood stream. The evidence, therefore, that there exists an important fluid-pathway from the subarachnoid space via the arachnoid villi into the dural sinuses appears extraordinarily strong and merits acceptance of Weed's conclusion that this is an important avenue of escape for cerebrospinal fluid. This conclusion also gains weight from Wegefarth's (1914) demonstration that in the eye the aqueous fluid gains access to the venous sinuses of the sclera through pectinate villi which are analogous in structure to the arachnoid villi. The hesitancy shown by some investigators to accept this explanation and the constant value of confirmatory data urge testing these conclusions with crystalloids other than the Prussian Blue reagents and, if possible, by a totally different method of experimentation.

The Nerve Roots

As has been mentioned, there is reason to believe that a relatively small quantity of cerebrospinal fluid finds its way into the lymphatic system. The pathway from the subarachnoid space has long been identified with the perineural spaces of the spinal and cranial nerves and from them to the lymphatics accompanying the nerves. Both Sabin (1912) and Weed (1914) have failed to find lymphatics in the meninges.

Early investigators, notably Key and Retzius (1876) in their classic studies on the cerebrospinal fluid, concluded that free communications exist between the subarachnoid space and the nerve roots so that cerebrospinal fluid drains directly into the substance of the nerves and the perineural spaces. Later work (see Elman, 1923) has conclusively demonstrated, however, that the subarachnoid space is completely closed, that the arachnoid membrane forms a short cuff about the emerging nerve roots and so isolates the subarachnoid space from any anatomical connection with tissues outside the central nervous system.

Weed (1914) has presented evidence of a functional connection between subarachnoid and perineural spaces. Using his ferrocyanide method for rather long periods and at low pressure, he found granules of Prussian Blue in the perineural spaces of spinal and cranial nerves. His material suggested diffusion of ferrocyanide into lymphatics lying beyond the outer, connective tissue wall of the space rather than direct absorption from the space.

As is implied above, it has been generally accepted that perineural spaces are normal structures accompanying the emerging nerves at least as far as the spinal ganglia. They have been described by Sabin (1912) in human and other embryos and many workers have claimed to have seen them in the adult (see Hassin, 1930b). After dehydrating his material by a special method, Elman (1923), however, found no evidence of them and suggested that they may be artifacts. Nor could he, after irrigating the subarachnoid space with ferrocyanide, demonstrate Prussian Blue granules in the perineural spaces made evident by the usual methods of dehydration.

How, then, if the perineural space be considered an artifact, may foreign solutions and cerebrospinal fluid escape from the spinal subarachnoid space? Elman de-

scribed clusters and columns of arachnoidal cells which invade the spinal dura mater in much the same way as the arachnoid villi described by Weed penetrate the cranial dura. These spinal arachnoid villi were found at the points where the arachnoid membrane was reflected onto the nerve roots and through them Prussian Blue granules could be traced into veins lying outside the meninges. Elman's material permitted no statement about lymphatic absorption. Wislocki and Kubie (1928) found plexuses of small venous sinuses in the spinal dura surrounding the emerging nerve roots. They suggested that the cerebrospinal fluid may drain into these small sinuses of the spinal dura mater via spinal arachnoid villi in just the way that the fluid flows through arachnoid villi into the venous sinuses of the cranial dura mater.

The most comprehensive opinion of absorption around the nerve roots, built on all the available evidence, suggests that small amounts of fluid pass into veins and lymphatics via perineural spaces and spinal arachnoid villi. The pathway in its details, however, is not clearly defined. The only route to the lymphatics for which there is evidence is by way of the perineural spaces and there is some doubt that these spaces are normal structures. There is the possibility, not yet investigated, that fluid may be absorbed by lymphatics lying outside the pachymeninx. It appears probable that small quantities of fluid gain access to the veins in or outside of the spinal dura mater. But again a definitive anatomic pathway has yet to be demonstrated. There are no observations to tell us whether the spinal arachnoid villi are related to veins in the same way as the cranial villi or whether fluid filters through them and then diffuses to neighboring veins either within or without the pachymeninx.

The Blood Vessels of the Subarachnoid Space

It is generally considered that the blood vessels traversing the subarachnoid space are not as small as arterioles and venules and that the leptomeninges are without an intrinsic capillary bed. Doubt exists as to whether or not these vessels receive a covering of mesothelial cells from the leptomeninges. According to Weed (1914) and others, as discussed above, such a covering is invariably present. Schaltenbrand and Bailey (1928), however, were unable to demonstrate such cells either lining the inner surface of the arachnoid membrane or covering the adventitia of the blood vessels. This is a point of importance, for knowledge of the presence or absence of a special cellular layer is fundamental to an understanding of the permeability of the blood vessels of the subarachnoid space.

Dandy and Blackfan (1914) concluded that the absorption of cerebrospinal fluid is a diffuse process taking place directly into the blood vessels of the entire subarachnoid space. They separated spinal from cranial subarachnoid space by ligation of the meninges, injected phenolsulphonphthalein into the spinal space and then recovered the dye from the urine. They reported, however, that absorption from the isolated spinal subarachnoid space was almost as great as from the combined cranial and spinal subarachnoid space. Howe (1929), without adding any valid experimental evidence, concurred in this opinion.

Exception to this view has been taken by Weed (1914 and 1922). He criticized the conclusions of Dandy and Blackfan on the basis of an obviously high cerebrospinal fluid pressure in their phenolsulphonphthalein experiments and possible leakage of the dye into the epidural tissues with direct absorption into the vessels there. He found, moreover, that absorp-

tion from the isolated cranial subarachnoid space was as rapid as from the total subarachnoid space and concluded that the cranial portion of the system contained the essential mechanism, the arachnoid villi, for absorption. These criticisms appear to the writer to lack finality. If dye absorption be accepted as a reliable index of cerebrospinal fluid absorption and possible toxic, diffusion and special absorption effects be neglected, a slightly elevated cerebrospinal fluid pressure such as likely occurred in the experiments of Dandy and Blackfan does not vitiate the demonstration of vessel permeability. Having demonstrated this, the force necessary for fluid exchange in the normal animal can be found in hydrostatic and possibly osmotic pressure differences between the cerebrospinal fluid and venous blood. Nor does it appear reliable to place emphasis on the quantitative disappearance of phenolsulphonphthalein from the subarachnoid space. The factor of error in such experiments has yet to be defined and, as Becht (1920) has contended, dye absorption cannot be taken as a quantitative index of cerebrospinal fluid absorption. Weed's failure to find Prussian Blue granules, after his replacement experiments, in the vessels of the subarachnoid space is not to be taken as conclusive evidence against their permeability to cerebrospinal fluid. It is well known (Stern and others) that the chorioid plexus and ventricular ependyma are impermeable to ferrocyanide though obviously permeable to cerebrospinal fluid; much the same possibility exists in the case of the vessels of the subarachnoid space.

It appears impossible to accept or reject the conclusions of Dandy and Blackfan. The evidence available, however, speaks weakly against a diffuse absorption of cerebrospinal fluid by the veins of the subarachnoid space. The experiments with dye absorption done in an isolated subarachnoid space have been made not only in the presence of the vessels of this space but in the presence of the spinal arachnoid villi. If, as is suggested by the work of Elman and Wislocki and Kubie, these villi are permeable to cerebrospinal fluid and through them fluid passes to the lacunae of the spinal dura, a mechanism is present for understanding the results of Dandy and Blackfan without making their assumptions. The quantitative data at hand are so small and so conflicting that they can fashion no conclusions. The situation is similar to that already found in the discussion of the permeability of the arteries of the subarachnoid space.

The Chorioid Plexus, Ventricular Ependyma and Perivascular Spaces

The conclusion of Askanazy (1914), Hassin (1930b) and others that the chorioid plexus normally absorbs certain constituents of cerebrospinal fluid has been discussed above and found based on experimental evidence of questionable meaning. The chorioid plexus has been implicated, however, in absorption which takes place under abnormal conditions, by investigators who ascribe no such function to it in the normal animal.

When the tonicity of the blood is increased by intravenous injections of hypertonic solutions, cerebrospinal fluid pressure undergoes a precipitous and sustained decrease. This finding has been taken as an indication of increased absorption of cerebrospinal fluid. Investigators have attempted to demonstrate new pathways of absorption caused by the changed osmotic pressure of the blood and, in particular, to probe the possibility that structures generally considered to elaborate the fluid can, under these special conditions, absorb it. Experiments along these lines, therefore, have to do with a decision

as to whether the membranes represented by the vessels, the cells of the chorioid plexus and ventricular ependyma and the structures of the perivascular spaces are permeable to the constituents of the cerebrospinal fluid in one direction only, i.e. from blood to fluid, or in both directions.

Nanagas (1921) injected the Prussian Blue reagents into the ventricles of kittens with experimental internal hydrocephalus and then gave hypertonic saline solutions intravenously. Under these conditions of optimum absorption, he failed to find precipitated Prussian Blue granules in the epithelial cells or vessels of the chorioid plexus. The same lack of evidence for absorption by the chorioid plexus was reported by Wislocki and Putnam (1921) who performed replacement experiments on hydrocephalic animals without using hypertonic solutions. Different results, however, were obtained by Foley (1921, 1923). He followed the Prussian Blue reagents through the chorioid plexus from its epithelial cells into its blood vessels. Forbes, Fremont-Smith and Wolff (1928), in well controlled experiments with Prussian Blue, have recently substantiated the results of Foley.

We are again faced with evidence difficult to evaluate. The work of Forbes, Fremont-Smith and Wolff, however, indicates that under special conditions the Prussian Blue reagents pass from the ventricles through the epithelial cells to the vessels of the chorioid plexus as first found by Foley. This passage of the Prussian Blue reagents through the plexus under the influence of hypertonic solutions is of peculiar interest. As has been mentioned, these reagents fail to pass through the plexus into the cerebrospinal fluid when they are introduced into the blood stream. We are therefore faced with the possibility that either the permeability of the plexus is different in one direction than in another or that hypertonic solutions actually alter the characteristics of the membrane. The last-named possibility appears to be the stronger.

Foley (1921 and 1923) also found evidence of absorption of cerebrospinal fluid by the ventricular ependyma when hypertonic solutions were given intravenously. The same picture was noted by Nanagas (1921) in hydrocephalic animals and he suggested further that this might be an avenue of minimal absorption in normal animals. Much the same results were reported by Wislocki and Putnam (1921) who traced the precipitated granules via the ependymal cells to intercellular and finally perivascular spaces. These experiments probably explain the findings of Dandy and Blackfan (1917). They injected phenolsulphonephthalein into the ventricles of human beings suffering from internal hydrocephalus and found small quantities of the dye appearing in the urine for many days.

Weed (1914) has demonstrated that Mott's (1910) suggestion of a normal pathway of absorption along the perivascular spaces is untenable. He has, however, very strong evidence that hypertonic solutions or experimental cerebral anemia cause a reversal of the normal direction of fluid-flow in the channels and that absorption then occurs. Absorption also takes place apparently directly into the blood vessels of the subarachnoid space after intravenous hypertonic salt.

The weight of evidence consequently appears to support the view that all the membranes identified with formation of cerebrospinal fluid can, under special conditions, absorb cerebrospinal fluid. The case for the perivascular spaces is strong; that for the chorioid plexus and ependyma, weaker. That hypertonic salt causes an important alteration in the character of

all the membranes is suggested by the evidence.

The studies discussed above indicate that normally the largest part of the cerebrospinal fluid is absorbed via the arachnoid villi into the great dural sinuses of the skull. It has been suggested on evidence still weak that fluid also finds its way into the blood stream through the veins of the subarachnoid space and the villi of the spinal arachnoid membrane. A relatively small amount of fluid is thought to drain into the lymphatics from perineural spaces or spinal arachnoid villi. The circulation of the fluid into the veins is presumably maintained by hydrostatic and possibly osmotic forces.

It has been evident throughout this discussion of the absorption of the cerebrospinal fluid that most of the data have come from following the pathways taken by the Prussian Blue reagents under various experimental conditions. Practically all of the present theory on absorption of the cerebrospinal fluid rests on these findings. It is imperative, therefore, that the method of investigation be subjected to as many critical tests as possible. A start in this direction is to be made by following the routes of drainage of crystalloids other than the Prussian Blue reagents from the subarachnoid space into the blood. Until information regarding the passage of other substances from the cerebrospinal fluid into the blood stream is obtained, the present theory of the pathway must remain with inadequate substantiation.

THE CIRCULATION OF THE CEREBROSPINAL FLUID

The generally accepted pathways of circulation of the cerebrospinal fluid have been reviewed by Weed (1922). Briefly, the fluid has been thought to flow from the ventricles into the cisterna magna and from here "slowly seeps downward in the spinal subarachnoid space but passes more rapidly upward about the base of the brain. . . ." The fluid gained by the subarachnoid space in this way receives a relatively very small addition from the perivascular spaces of the central nervous system. In the past ten years some hypotheses and some experimental data have been added to this picture; but, from a quantitative viewpoint, it is still far from complete.

C. v. Monakow (1921) has proposed a pathway of circulation of the cerebrospinal fluid which has provoked considerable discussion. According to him, the ventricular fluid formed by the chorioid plexuses passes through the ventricular ependyma, penetrates into the substance of the hemispheres, and arrives, in part with aid of the neuroglia, in contact with the cerebral parenchyma which it nourishes. The fluid then flows into pericellular spaces and from these via the perivascular spaces into the subarachnoid space. It is consequently possible to distinguish between an afferent fluid from the ventricles to the nerve cells and an efferent fluid from the pericellular spaces through the subarachnoid space to the sites of fluid-absorption (see Stern and Gautier, 1922/23).

This hypothesis has been accepted, among others, by Stern and her coworkers. Stern (1921), Stern and Gautier (1922/23) and Stern and Rapoport (1928) have investigated the passage of foreign solutions from ventricles and subarachnoid space to the tissues of the brain. Excitatory effects have, with few exceptions, been found to be much greater after injection of toxic, foreign solutions into the ventricles than after their injection into the subarachnoid space. In many instances, injection into the subarachnoid space was without detectable effect unless the injection-pressure was high enough to force the foreign substance into the ventricles. This is evi-

dence against the objection that possible escape of the toxic solution into the needle-wound made in the brain by ventricular puncture accounts for the excitatory effects of ventricular injections. Crystalloid dyes introduced into the subarachnoid space failed to stain the nerve tissue. Their introduction into the ventricles, however, produced staining of ependymal, neuroglial and ganglion cells and dye was also found in the pericellular and perivascular spaces and within the arterioles and capillaries, not only of the ventricular wall, but of the cortical surface as well. Similar results have been reported in normal and hydrocephalic animals by Nanagas and Wislocki and Putnam as is noted above. In the view of v. Monakow and Stern these results mean that foreign substances are carried by the cerebrospinal fluid from the ventricles to the cells of the brain; that cerebrospinal fluid circulates from the ventricles into and across the parenchyma of the hemispheres.

This viewpoint has been questioned by Walter (1926) who argued that it is based on incomplete anatomical and physiological evidence and that it cannot be applied to the spinal cord, the central canal of which is without an active circulation of cerebrospinal fluid. Gärtner (1927) remarked that the pressure gradient between fluid in the ventricles and subarachnoid space is probably too small to account for any more than a minimal circulation across the resistance offered by the tissues of the central nervous system. The experiments reported by Stern and her coworkers, by Nanagas (1921) and by Wislocki and Putnam (1921) demonstrate primarily a difference in reaction of the connective tissue elements of the leptomeninges lining the subarachnoid space and of the ventricular ependyma to foreign solutions. This contrast in reaction may be related wholly to inequalities in the toxicity of the foreign substance for connective tissue and ependymal cells, and to differences in diffusion rate of the foreign substance across these cells. It may be without relationship, consequently, to the normal pathway in which the cerebrospinal fluid circulates. The evidence that ependyma has to do with the formation of cerebrospinal fluid is at least as strong as that tending to show that it absorbs and the two functions are difficult to reconcile. The large accumulation of fluid under high pressure which occurs in internal hydrocephalus speaks most forcefully against this viewpoint. Nor is it sufficient, having demonstrated that cells are permeable to the constituents of the cerebrospinal fluid, to conclude that an active circulation occurs across them. Certainly the weight of evidence favors the view that practically all of the cerebrospinal fluid leaving the ventricles gains access to the subarachnoid space without traversing the mass of the central nervous system.

Numerous observations favor the view that there is a definitive current of cerebrospinal fluid flowing from the ventricles through the foramina of Luschka and perhaps the foramen of Magendie into the subarachnoid space. A fair sample of the evidence can perhaps be given by mentioning that Stern and Gautier (1922/23) regularly and rapidly detected substances in the subarachnoid space after their injection into the ventricles. Only rarely, moreover, did substances injected into the subarachnoid space appear in the ventricles and some of these cases are perhaps to be explained by failure to control adequately the fluid-pressure in the subarachnoid space. Schaltenbrand and Putnam (1927), after injecting fluorescine intravenously, observed the dye escaping from the fourth ventricle into the subarachnoid space. It is interesting to note that there was no evidence of fluid-flow through the "for-

amen of Magendie" in cats, dogs or rabbits so that the existence of this communication in these animals has been doubted.

The rate of flow of cerebrospinal fluid from the aqueduct of Sylvius has been measured in etherized cats by Flexner and Winters (1932). In these experiments the fourth ventricle was blocked with a distended rubber balloon. The fluid escaping from the aqueduct was conducted to a bubble-manometer under normal intraventricular pressure by means of a catheter introduced into and through the balloon. It was found that an average of 12 cc. per day of cerebrospinal fluid escaped from the aqueduct. In many animals the rate of flow was highly irregular. Periods of active flow were followed by phases in which no fluid left the aqueduct or in which increase in ventricular volume aspirated fluid from the manometer into the ventricle.

If a correction were made for the cerebrospinal fluid presumably formed by the chorioid plexus of the fourth ventricle, it was found that approximately 0.6 cc. of fluid per hour flowed into the subarachnoid space of the cat. This is obviously a rate of circulation of a very small magnitude. In view of this and the observation that no fluid may leave the aqueduct during certain periods or that fluid may be actually aspirated into the ventricles, it is not surprising that investigators have noted that on occasion dyes introduced into the subarachnoid space have appeared within the ventricles. These factors probably account for the conclusions of Sachs, Wilkins and Sams (1930). These investigators, after studying the diffusion rate of trypan blue in vitro, injected the dye into a lateral ventricle and noted the time necessary for its appearance in the cisterna magna. They concluded that there was no directional current between the ventricles and the subarachnoid space and that the dye spread simply by diffusion.

Many efforts have been made to gain a measure of the rate of circulation in the spinal subarachnoid space. The conclusion of Dandy and Blackfan (1914) that the fluid is removed every four or six hours is based on the rate of absorption of phenolsulphonphthalein. The method has been adequately criticized by Becht (1920): from the results obtained with it nothing can be said of the rate of absorption of the fluid. Sachs, Wilkins and Sams (1930) injected trypan blue into the lumbar subarachnoid space and concluded that the dye spread only by diffusion. Jacobi (1923) concluded there is no true circulation in the spinal subarachnoid space after finding rather constant differences in the protein content of the fluid at various levels of the spinal subarachnoid space. Much the same conclusion was reached by Becher (1921). He believed, however, that there is minimal movement and mixing of the fluid in the spinal subarachnoid space resulting from the rhythmic changes in brain volume which follow cardiac systole and respiration. Recent work (Weed, Flexner and Clark, 1932) indicates that some movement of fluid also follows change in position of the animal; if its position be changed from the horizontal, fluid is dislocated from the uppermost to the dependent portions of the subarachnoid space. Walter (1926), who appears to favor the view that the blood vessels of the subarachnoid space take part in the formation and absorption of the fluid, suggests that in the spinal subarachnoid space formation and absorption of the fluid takes place principally in horizontal planes at places very near to one another. These observations are perhaps representative of the evidence which has led investigators to consider the spinal subarachnoid space without a true circulation.

This conclusion finds substantiation in the observations, mentioned above, on the rate of escape of cerebrospinal fluid

from the aqueduct of Sylvius. There appears to be, in the cat, a definitive movement of fluid from the ventricles to the subarachnoid space. The rate of fluid flow into the cisterna magna is, however, at its maximum extremely small and may, during short intervals, be zero or a negative value due to aspiration of fluid from the subarachnoid space by dilating ventricles. The rate of circulation in the subarachnoid space must in consequence be of a very low magnitude. This accounts for the persistence of differences in chemical constitution of the cerebrospinal fluid at different levels and for the importance of diffusion in the spread of foreign substances injected into the fluid. More exact statements await the determination of the volume of the subarachnoid space, a quantity which has yet to be well measured. It is perhaps fair to add, however, that due to its greater absorbing surface, more fluid passes through the cranial than through the spinal subarachnoid space.

THE BARRIER BETWEEN BLOOD AND CEREBROSPINAL FLUID

It is well known that many foreign substances introduced into the blood stream do not escape into the cerebrospinal fluid or central nervous system. To the mechanism responsible for this protection of the nervous system, Ehrlich gave the name of barrier. Subsequent thought attempted a more specific designation with the result that passage of substances from blood to cerebrospinal fluid was identified with the permeability of the leptomeninges. Failure of a substance to pass from blood to fluid or nervous system was attributed to impermeability of the meninges and the whole subject was, and often is still today, considered under the title of meningeal permeability.

Among others, Stern (1923) has objected to the use of this term. Although admitting the impossibility of identifying precisely the anatomical substratum of the barrier, she concluded that neuroglia, ependyma, chorioid plexus and vascular endothelium all were likely involved in addition to the meninges and she proposed the term "Barrière Hémato-encéphalique." Walter (1929) is one of many of the German school who, like Stern, prefers to retain the inclusiveness of Ehrlich's term and writes of the "Blut-Liquorschranke." Zylberlast-Zand (1924), however, concluded that the term meningeal permeability is exact in its implications. Justification of any particular designation quite obviously must come from consideration of anatomical and physiological studies having to do with the nature of the membranes between the blood and the central nervous system.

The approach of choice to the physicochemical nature of membranes placed between the arterial blood and central nervous system involves a comparative study of the chemistry of blood and cerebrospinal fluid. This is a long and complex subject, however, and will be discussed elsewhere (Flexner, 1934). We shall consider here briefly experimental data concerning the passage of a few foreign substances from blood to fluid and the evidence available on the anatomical substratum of the barrier.

Stern and her coworkers (Stern, 1921; Stern and Gautier, 1921–22; Stern and Rapoport, 1927a) have published many experimental data on the passage of substances from blood to cerebrospinal fluid and nervous system. It has been their object, in part, to determine whether the physical properties of size and charge of particles introduced into the blood account for their behavior at the barrier. This has been tested most simply by comparing results obtained with groups of substances, each group being composed of members with certain physical properties of assumed equivalence. Stern has concluded

that no chemical law offers an explanation of the function of the barrier. Anions such as bromide and chloride pass into the cerebrospinal fluid from the blood with ease; iodide, though highly diffusible, is to be found in the fluid only in very small amounts even though its blood concentration be high.

Using a large series of dyes and inorganic compounds, Wittgenstein and Krebs (1926) came to the conclusion that all anions pass the barrier from blood to cerebrospinal fluid. Their series included ferrocyanide and Orange G, with which Stern and others have had negative results. Basic dyes, however, were not to be found in the cerebrospinal fluid, nor did colloidal dyes pass the barrier. The results of Wittgenstein and Krebs show complete uniformity in the behavior of a particular group of substances. Ions having a positive charge are adsorbed by the negatively charged proteins of the plasma and are not available for passage across the barrier. Negatively charged ions, free in the blood plasma, pass the barrier. Colloids, because of their size, fail to go into the cerebrospinal fluid. These results find disagreement not only in the findings of Stern but also in the work of Wesselkin (1930). Wesselkin found that certain acid dyes failed to pass the barrier whereas basic dyes stained the central nervous system.

These results are sufficient to indicate that very little is known of the exact behavior of the barrier to foreign substances in the blood. Nor is this surprising. The method of investigation lacks refinement. Too little account has been taken of the dosage of foreign substances injected into the blood and of the maximal limit of concentration beyond which toxic effects produce an abnormal barrier. No effort has been made to test the permeability of the barrier in these experiments and to prove it unaltered for normal or abnormal constituents of the blood. Nor has the state of these foreign substances in the plasma been determined. Each and all of these factors must be known before the function of the barrier can be understood and an almost complete lack of understanding at the moment makes futile an attempt to evaluate the available data.

It is of interest to note at this point that all crystalloids placed in the subarachnoid space quickly appear in the blood stream. Ferrocyanide, not detected by most investigators in the cerebrospinal fluid when present in the blood, rapidly passes from the fluid into the blood. The membranes placed between the arterial blood and the central nervous system are quite clearly different than those separating the cerebrospinal fluid and the venous blood. In the understanding of the behavior of these membranes lies the understanding of the mechanism by which the central nervous system is protected from noxious substances and by which it rids itself of such substances—a subject of fundamental importance in the physiology, pathology and therapeutics of the central nervous system.

Three principal concepts have been advanced as to the anatomical substratum of the barrier. It is clear that variation of opinion must come in part at least from the several divergent views of the origin of the cerebrospinal fluid. Wherever fluid is formed, membranes must be placed between it and the blood; the tissues of the barrier will be more numerous, the greater the number of assumed sites of fluid-formation. The simplest concept considers the epithelium of the chorioid plexus identical with the barrier. The old theory of a true meningeal permeability also has its adherents. The most comprehensive view involves the functional synergy of many tissue elements including the epithelium of the chorioid plexuses, the ependyma of the ventricles, the endo-

thelium of the cerebral capillaries and the neuroglia placed between the blood vessels and the nerve cells.

Mestrezat (1912) considered the chorioid plexuses alone to regulate the composition of the cerebrospinal fluid. This view has been substantiated by observations first made by Goldmann (1913), in which trypan blue was found in the epithelial cells of the plexus and the adventitial cells of the blood vessels after intravenous injection, though it was missing in the cerebrospinal fluid. When the dye was placed directly into the ventricles, however, Goldmann found that it passed through the ependyma to underlying cells, indicating that the ependyma is not a barrier to its passage as are the epithelial cells of the plexus. These observations of Goldmann have been frequently confirmed (see Gärtner, 1927) and have led to rather wide acceptance of the view that the chorioid plexus is a selective filter through which certain substances cannot pass from blood to central nervous system.

The work of Zylberlast-Zand (1924) has directed attention anew to a true meningeal permeability. This author, like other investigators, has identified histiocytes in all the connective tissue elements of the central nervous system and it is her theory that these histiocytes constitute the barrier between blood and cerebrospinal fluid. The theory has as one of its important foundations an experiment carried out on several kinds of animals. Trypan blue, given intravenously, failed to stain the nervous tissue of the normal animal. If, however, the superficial pia mater was destroyed by scarification or freezing, the brain beneath it became stained. Hence, presumably, a demonstration of the protective rôle of the pia mater and its histiocytes. In such experiments, however, the pia mater in all probability is not changed alone; the walls of the blood vessels of the area are likely damaged and their permeability greatly altered. The experimental basis for the theory is consequently inadequate. The hypothesis for this reason and because of several untenable implications cannot be considered acceptable. It has its value, however, in directing attention to the histiocytes of the mesodermal tissues of the central nervous system as a possibly important part of the anatomical substratum of the barrier.

Cestan, Laborde and Riser (1925) injected foreign substances into the blood and a short time later found them in practically equivalent concentrations in fluid from the lumbar subarachnoid space and the cisterna magna. They appreciated the dangers of artifacts and attempted their elimination. The conclusion drawn from these results is that the blood vessels throughout the subarachnoid space and central nervous system in addition to the chorioid plexuses, regulate the passage of substances from the blood. Meningeal permeability, according to these authors, merits its name though fundamentally it is to be regarded simply as a vascular permeability. These results are so far reaching in their implications that they call for confirmation.

The first element in the barrier was considered by Gärtner (1927) to be the walls of the blood vessels. Substances having passed the vessels encountered either the most important part of the barrier, the epithelial edge of the chorioid plexus, or the largest part of the barrier, the membrana limitans gliae. This glial "membrane," placed between the nervous tissue and the connective tissue of its blood vessels, was considered by Gärtner to be present in practically all regions of the brain between ectoderm and mesoderm. Its relationship to the barrier was first indicated by the escape of trypan blue

where it was lacking; for example, from the blood vessels into the ectodermal tissue of the posterior lobe of the hypophysis, and the complete protection of tissues when it was present. Puncture wounds of the brain were made and at various periods thereafter trypan blue was given intravenously. Much staining of the mesodermal-glial granulation tissue always followed; staining of the ectodermal tissue was never noted. The glial membrane, therefore, in Gärtner's view is a part of the barrier to passage of colloids from the blood. It is to be regarded not only as a boundary between mesoderm and ectoderm but also between the colloid-containing blood plasma and the colloid-free cerebrospinal fluid.

A very comprehensive view of the tissue elements composing the barrier has been advanced by Stern and her coworkers (see Stern, 1929). In it, as has been mentioned, are included all the cells which form the boundary between mesoderm and ectoderm; the epithelium of the chorioid plexuses, the ependyma of the ventricles, the walls of the cerebral blood vessels, the neuroglia.

It was noted by Stern and Rapoport (1927b) and by Stern and other of her collaborators (see Stern, 1929) that experimental alterations in the character of the barrier might affect its permeability for colloids without affecting its permeability for crystalloids or, conversely, an alteration in crystalloid-permeability might occur without change in colloid-permeability. Thus in the newly born animal, unlike the adult, the crystalloid, ferrocyanide, passed the barrier whereas trypan blue failed to enter the central nervous system. In cases of experimental carbon monoxide poisoning or thyroidectomy, permeability for crystalloids remained unchanged while permeability for colloids increased. After increasing the osmotic pressure or pH of the blood, there was evidence of an increase in permeability for all types of substance. Findings of this sort led to the interesting speculation that two different sets of anatomical elements governed the permeability to crystalloids and colloids.

There followed an attempt to verify this hypothesis histologically. The histological picture after escape of a foreign crystalloid into the central nervous system was entirely different than after escape of a colloid. Ferrocyanide, having escaped into the cerebrospinal fluid, was to be identified as Prussian Blue granules principally within the epithelial cells of the chorioid plexuses which usually showed pathological changes. Prussian Blue was also to be seen in the walls of the ventricles, but never in the walls of the blood vessels of the central nervous system. Trypan blue, on the other hand, having escaped into the cerebrospinal fluid, was to be found in the walls of the blood vessels and in the perivascular spaces. The findings suggested that the passage of trypan blue was to be related to alterations in the permeability of the blood vessel walls whereas ferrocyanide entered the central nervous system because of a change in the permeability of chorioid plexus and ependyma. The regulation of the passage of crystalloids into the cerebrospinal fluid was consequently attributed in large part to the chorioid plexus; the regulation of the passage of colloids, to the cells of the vessel walls.

The investigation of the anatomical substratum of the barrier has produced contradictory opinions as have the studies of its function. There is evidence that entering into its formation are histiocytes, glia, ependyma, the epithelium of the chorioid plexuses and the tissues of the blood vessels. Nor is this surprising. All these cells have been known to ob-

struct the passage of colloidal dyes across them. The situation loses its clarity, however, when we question the quantitative part played by each of the constituents. Most investigators stress the importance of the epithelium of the chorioid plexuses—and this is in agreement with our present theories of fluid-formation. Others, however, point to the histiocytes, glia or blood vessels as furnishing the important membranes. It is well to leave this a problem open for future work to be guided but not too much influenced by the work of the past. So too with the problem raised by Stern—the possible difference in the morphological basis for impermeability to certain crystalloids and to colloids.

THE FUNCTIONS AND SIGNIFICANCE OF THE CEREBROSPINAL FLUID

The cerebrospinal fluid has long been regarded as affording protection to the central nervous system. It helps to support the weight of the brain, tends to distribute equally the force of blows, serves as a lubricant between the bony axis and the brain and spinal cord (Aycock, 1925). In addition to these rather obvious purposes, it has another important mechanical function. The skull and vertebral column have a capacity which is practically constant and both are completely filled with central nervous system, blood and cerebrospinal fluid. Variation in the volume of any one of these constituents must be met by reciprocal compensation in the volumes of the others. The cerebrospinal fluid, therefore, through alterations in its quantity, permits changes in the volume of the central nervous system and the vascular bed within the bony axis (Flexner, Clark and Weed, 1932). Because changes in its volume probably occur relatively slowly, it serves to protect the central nervous system from sudden changes in the amount of blood coming to it.

A problem of major interest revolves about the relation of the cerebrospinal fluid to the metabolism of the nerve cells. Many authors have considered it to bring nourishment to the nerve cells and to carry their metabolites away. Such a view, for example, is the inevitable consequence of von Monakow's schema of the intracerebral circulation of the fluid discussed above. To present here the various contradictory opinions which have grown up about this point would simply involve a reëxamination of the anatomical and physiological data already presented. We shall consider, therefore, only that point of view which appears to fit best the acceptable experimental findings.

All the organs of the body, excepting the central nervous system, have lymphatics. It is a function of these vessels to drain away that part of the tissue fluid with its metabolites not returned directly to the blood. The lymphatics are consequently a most important link in the regulation of fluid distribution. The perivascular spaces appear to fill this need within the brain and spinal cord. Fluid leaves the capillaries of the central nervous system to nourish its cells, and that part, with its products of metabolism, not returned directly to the blood, flows through the perivascular spaces to the subarachnoid space.

The larger quantity of cerebrospinal fluid coming from the ventricles can nourish only those cells which border upon its pathway of circulation—the ependyma of the ventricles, the cells of the leptomeninges and possibly, in an incomplete way, a thin layer of cells lying below those named. The ventricular fluid probably performs the more important function of washing into the venous system the products of tissue metabolism which are

discharged into the subarachnoid space from the perivascular spaces.

It is perhaps worth while to conclude this review by pointing out that the cerebrospinal fluid presents problems of physiological and clinical interest not fully considered here. It must be given a major part in all comprehensive discussions of intracranial pressure and intracranial circulation. An understanding of the chemistry of the fluid and its mode of separation from the blood is necessary to the better understanding of the membranes of the body and to the problem of fluid distribution within the body. In this connection and in others, it must be emphasized that practically all that is known of the fluid has come from studies on mammals. There are but few investigations on submammalian forms from which much might be contributed to a better understanding of all of its problems.

Beyond the clinical interest of disorders such as hydrocephalus, knowledge of the rate and pathways of circulation, of the absorption and mode of origin of the fluid is needed for intelligent therapeutic measures within the central nervous system. For though the brain is guarded by the absence of a true lymphatic system continuous with that of the rest of the body and by special membranes placed about its vessels, it is, because of this protection, inaccessible to many of our weapons against disease carried to other organs by the blood.

LIST OF LITERATURE

ADAMKIEWICZ, A. 1882. Die Gefässe der Rückenmarkes-oberfläche. *Sitzungsberichte der k. Akad. d. Wiss. in Wien. Math.-naturw. Cl.*, 85, pt. 3: 101.

ASKANAZY, M. 1914. Zur Physiologie und Pathologie der Plexus chorioidei. *Verhandl. der Deuts. Path. Gesellsch.*, 17: 85.

AYCOCK, W. L. 1925. Cerebrospinal fluid pressure. *Arch. Neur. & Psych.*, 14: 251.

BECHER, E. 1921. Zur Frage der Liquorströmung im spinalen Arachnoidealsack. *Münch. Med. Wochenschr.*, 68: 839.

BECHT, F. C. 1920. Studies on the cerebrospinal fluid. *Am. Jour. Physiol.*, 51: 1.

BECHT, F. C., and GUNNAR, A. H. 1921. Studies on the cerebrospinal fluid. A study of the volume changes of the cerebrospinal fluid after adrenalin, pituitrin, pilocarpine and atropine. *Am. Jour. Physiol.*, 56: 231.

CESTAN, LABORDE, and RISER. 1925. La perméabilité méningée n'est qu'un des modes de la perméabilité vasculaire. *Press. Méd.*, 33: 1330.

COUPIN, F. 1930. Les formations choroidiennes des poissons et la question de l'origine du liquide cephalorachidien. *Schweiz. Arch. f. Neur. & Psych.*, 26: 227.

CUSHING, H. 1914. Studies on the cerebrospinal fluid. *Jour. Med. Research*, 26: 1.

———. 1925. Cameron Lectures. I. The third circulation and its channels. *Lancet*, 209: 851.

DANDY, W. E. 1919. Experimental hydrocephalus. *Ann. Surg.*, 70: 129.

DANDY, W. E. 1929. Where is cerebrospinal fluid absorbed? *Jour. Am. Med. Assoc.*, 92: 2012.

DANDY, W. E., and BLACKFAN, K. D. 1914. Internal hydrocephalus. *Am. Jour. Dis. Child.*, 8: 406.

———. 1917. Internal hydrocephalus. *Am. Jour. Dis. Child.*, 14: 424.

DAVIS, L. E. 1923–24. A physio-pathologic study of the chorioid plexus with the report of a case of villus hypertrophy. *Jour. Med. Research*, 44: 521.

ELMAN, R. 1923. Spinal arachnoid granulations with especial reference to the cerebrospinal fluid. *Johns Hopkins Hosp. Bull.*, 34: 99.

ESSICK, C. R. 1920. Formation of macrophages by the cells lining the subarachnoid cavity in response to the stimulus of particulate matter. *Contrib. to Embryol.*, No. 42, *Publication* 272 *of the Carnegie Institution of Washington.*

FLEXNER, L. B. 1929. The development of the meninges in amphibia. A study of normal and experimental animals. *Contrib. to Embryol.* 110, *Publ.* 394, *Carnegie Inst. Wash.*, p. 31.

———. 1934. In preparation.

FLEXNER, L. B., CLARK, J. H., and WEED, L. H. 1932. The elasticity of the dural sac and its contents. *Am. Jour. Physiol.*, 101: 292.

FLEXNER, L. B., and WINTERS, H. 1932. The rate of formation of cerebrospinal fluid in etherized cats. *Am. Jour. Physiol.*, 101: 697.

FOLEY, F. E. B. 1921. Resorption of the cerebrospinal fluid by the chorioid plexus under the

influence of intravenous injections of hypertonic salt solutions. *Arch. Neur. & Psych.*, 5: 744.

FOLEY, F. E. B. 1923. Alterations in the currents and absorption of cerebrospinal fluid following salt administration. *Arch. Surg.*, 6: 587.

FORBES, H. S., FREMONT-SMITH, F., and WOLFF, H. G. 1928. Resorption of cerebrospinal fluid through the chorioid plexus. *Arch. Neur. & Psych.*, 19: 73.

GÄRTNER, W. 1927. *Zeits. f. Biol.*, 86: 115.

GOLDMANN, E. E. 1913. Vitalfärbung am Zentralnervensystems. Verlag d. Königl. Akad. d. Wissensch., *Berlin*.

HALLIBURTON, W. D. 1916. The possible functions of the cerebrospinal fluid. *Proc. Roy. Soc. Med. (Section of Neurology)*, 10: 1.

HASSIN, G. B. 1930a. Hydrocephalus. *Arch. Neur. & Psych.*, 24: 1164.

———. 1930b. Villi (Pacchionian bodies) of the spinal arachnoid. *Arch. Neur. & Psych.*, 23: 65.

HASSIN, G. B., ISAACS, H., and COTTLE, M. 1922. Clinical pathologic report of a case of pons haemorrhage (Type Foville). *Jour. Nerv. & Ment. Dis.*, 56: 553.

HELD, H. 1909. Über die Neuroglia marginalis der menschlichen Grosshirnrinde. *Monatschr. f. Psych.*,26.

HIS, W. 1865. Über ein perivaskuläres Kanalsystem in den nervösen Zentralorganen und über dessen Beziehungen zum Lymphstrom. *Ztschr. f. wiss. Zool.*, 15: 127.

HOWE, H. S. 1929. Physiological mechanism for the maintenance of intracranial pressure. In "The Intracranial Pressure in Health and Disease." *Baltimore*, p. 7.

HUDACK, S. S., and MCMASTER, P. D. 1931. The breakdown of lymph transport. *Proc. Soc. Exper. Biol. & Med.*, 28: 853.

———. 1932. The gradient of permeability of the skin vessels as influenced by heat, cold and light. *Jour. Exp. Med.*, 55: 431.

JACOBI, W. 1923. Bestehen Unterschiede im Eiweissgehalt des Liquor cerebrospinalis in verschiedenen Höhen? *Münch. Med. Wochenschr.*, 70: 870.

KADYI, H. 1889. Über die Blutgefässe des menschlichen Rückenmarkes. *Lemberg*, Gubrynowicz & Schmidt.

KAPPERS, C. U. A. 1926. Meninges in lower vertebrates compared with those in mammals. *Arch. Neur. & Psych.*, 15: 281.

KEY, A., and RETZIUS, G. 1876. Studien in der Anatomie des Nervensystems und des Bindegewebes. *Stockholm*.

KLESTADT, B. 1915. Experimentelle Untersuchungen über die resorptive Funktion des Epithels des Plexus choroideus und des Ependyms der Seitenventrikel. *Centralbl. f. allg. Path. u. Path. Anat.*, 26: 161.

KUBIE, L. S., and SCHULTZ, G. M. 1925. Vital and supravital studies of the cells of the cerebrospinal fluid and of the meninges in cats. *Bull. Johns Hopkins Hosp.*, 37: 91.

LE GROS CLARK, W. E. 1920–21. On the Pacchionian bodies. *Jour. Anat.*, 55: 40.

MAGNUS, G., and JACOBI, W. 1925. Über den Liquor cerebrospinalis und das Hirnödem. *Arch. f. Klin. Chir.*, 136: 652.

MALLORY, F. B. 1920. The type of cell of the so-called dural endothelioma. *J. Med. Research*, 41: 349.

MESTREZAT, W. 1912. Le Liquide Céphalo-Rachidien. *Paris*.

MONAKOW, C. v. 1921. Der Kreislauf des Liquor cerebrospinalis. *Schweiz. Arch. f. Neur. & Psych.*, 8: 233.

MOTT, F. W. 1910. The Oliver-Sharpey lectures on the cerebrospinal fluid. *Lancet*, Part II: 1 and 79.

NANAGAS, J. C. 1921. Experimental studies on hydrocephalus. *Johns Hopkins Hosp. Bull.*, 32: 381.

PAPILIAN, V., and STANESCO JIPPA, V. 1925. Recherches expérimentales sur la circulation du liquide céphalorachidien. *J. Physiol. et Path. gén.*, 23: 769.

PESTALOZZI. 1849. Über Aneurysmata spuria der kleinen Gehirnarterien und ihren Zusammenhang mit der Apoplexie. Inaug.-Abhandl. *Würtzburg*.

POIRIER, P., and CHARPEY, A. 1892–1902. Traité d'Anatomie Humaine. *Paris*, Battaille.

RISER, R., and SOREL. 1928. L'origine du liquide céphalorachidien. *Press. Méd.*, 36: 1123.

ROBIN, C. 1859. Recherches sur quelques particularités de la structure des capillaires de l'encéphale. *Jour. de la physiol. de l'homme et des animaux*, 2: 537.

ROTH, M. 1869. Zur Frage von der Bindesubstanz in der Grosshirnrinde. *Virch. Arch.*, 46: 243.

ROUS, P., GILDING, H. P., and SMITH, F. 1930. The gradient of vascular permeability. *Jour. Exp. Med.*, 51: 807.

SABIN, F. R. 1912. In Keibel and Mall, "Human Embryology."

SACHS, E., WILKINS, H., and SAMS, C. F. 1930. Studies on cerebrospinal circulation by a new method. *Arch. Neur. & Psych.*, 23: 130.

SCHALTENBRAND, G. 1928. Die Physiologie und Pathologie der Liquorzirkulation. *Münch. Med. Wochenschr.*, 75: 1584.

SCHALTENBRAND, G., and BAILEY, P. 1928. Die

perivaskuläre Piagliamembran des Gehirns. *Jour. f. Psych. & Neur.*, 35: 199.

SCHALTENBRAND, G., and PUTNAM, T. 1927. Untersuchungen zum Kreislauf des Liquor cerebrospinalis mit Hilfe intravenöser Fluoreszineinspritzungen. *Deut. Ztschr. f. Nervenheilk.*, 96: 123.

SMITH, F., and ROUS, P. 1931. The gradient of vascular permeability. IV. The permeability of the cutaneous venules and its functional significance. *Journ. Exp. Med.*, 54: 499.

SPIELMEYER, W. 1922. Histopathologie des Nervensystems. Bd. 1, *Berlin.*

SPINA, A. 1899. Experimentelle Untersuchungen über die Bildung des Liquor cerebrospinalis. *Pflüg. Arch. f. Physiol.*, 76: 204.

STERN, L. 1921. Le liquide céphalorachidien au point de vue de ses rapports avec la circulation sanguine et avec les éléments nerveux de l'axe cérébrospinal. *Schweiz. Arch. f. Neur. & Psych.*, 8: 215.

———. 1923. La barrière hémato-encéphalique en physiologie et en clinique. *Schweiz. Med. Wchnschr.*, 4: 792.

———. 1929. Les dernières recherches concernant le functionnement de la barrière hémato-encéphalique. *Schweiz. Med. Wchnschr.*, 59: 935.

STERN, L., and GAUTIER, R. 1921–22. Les rapports entre le liquide céphalo-rachidien et les éléments nerveux de l'axe cérébrospinal. *Arch. Internat. de Physiol.*, 17: 391.

———. 1922–23. Recherches sur le liquide céphalorachidien. *Arch. Internat. de Physiol.*, 20: 403.

STERN, L., and RAPOPORT, J. 1927a. À propos du méchanisme du passage de diverses substances du sang dans le liquide céphalorachidien. *Compt. Rendu Soc. de Biol.*, 97: 366.

———. 1927b. La résistance de la barrière hématoencéphalique au passage de colloides du sang dans le liquide céphalorachidien aux divers stades de développement chez les divers espèces animals. *Compt. Rendu Soc. de Biol.*, 96: 1149.

———. 1928. Les échanges entre le liquide céphalorachidien et les éléments nerveux cérébrospinaux. *Compt. Rendu Soc. de Biol.*, 98: 1518.

VIRCHOW, R. 1851. Über die Erweiterung kleiner Gefässe. *Virch. Arch.*, 3.

WALTER, F. K. 1926. Wo entsteht der Liquor cerebrospinalis? *Deut. Ztschr. f. Nervenheilk.*, 90: 161.

———. 1929. Die Blut-Liquorschranke: Eine physiologische und klinische Studie. *Leipzig.*

WEED, L. H. 1914. Studies on cerebrospinal fluid. No. II. The theories of drainage of cerebrospinal fluid with an analysis of the methods of investigation. No. III. The pathways of escape from the subarachnoid spaces with particular reference to the arachnoid villi. No. IV. The dual source of cerebrospinal fluid. *Jour. Med. Research*, 31: 21, 51 and 93.

WEED, L. H. 1917. The development of the cerebrospinal spaces in pig and in man. *Contribs. to Embryol.*, No. 14, *Publication* No. 225. *Carnegie Inst. of Washington.*

———. 1922. The cerebrospinal fluid. *Physiol. Reviews*, 2: 171.

———. 1923. The effects of hypotonic solutions upon the cell-morphology of the choroid plexuses and central nervous system. *Am. Jour. Anat.*, 32: 253.

WEED, L. H., FLEXNER, L. B., and CLARK, J. H. 1932. The effect of dislocation of cerebrospinal fluid upon its pressure. *Am. Jour. Physiol.*, 100: 246.

———. 1933. Positional adjustments of the pressure of the cerebrospinal fluid. *Physiol. Reviews*, 13: 80.

WEGEFARTH, P. 1914. Studies on cerebrospinal fluid. V. The drainage of intra-ocular fluids. *Jour. Med. Research*, 31: 119.

WESSELKIN, P. N. 1930. Versuche über die Durchlässigkeit der Gefässe des Auges und Gehirnes für saure und basische Farbestoffe. *Zts. f. die Ges. Exp. Med.*, 72: 90.

WINKELMAN, N. W., and FAY, T. 1930. The Pacchionian system: Histologic and pathologic changes with particular reference to the idiopathic and symptomatic convulsive states. *Arch. Neur. & Psych.*, 23: 44.

WISLOCKI, G. B., and KUBIE, L. S. 1928. The cytology of the cerebrospinal pathway. In Cowdry's "Special Cytology," vol. II, p. 1071.

WISLOCKI, G. B., and PUTNAM, T. J. 1921. Absorption from the ventricles in experimentally produced internal hydrocephalus. *Am. Jour. Anat.*, 29: 313.

———. 1924. Further observations on the anatomy and physiology of the areae postremae. *Anat. Rec.*, 27: 151.

WITTGENSTEIN, A., and KREBS, H. A. 1926. Studien zur Permeabilität der Meningen unter besonderer Berücksichtigung physikalisch-chemischer Gesichtspunkte. *Zts. f. die ges. Exp. Med.*, 49: 553.

WOOLLARD, H. H. 1924. Vital staining of the leptomeninges. *Jour. Anat.*, 58: Part 2, 89.

WÜLLENWEBER, G. 1924. Über die Funktion des Plexus choroideus und die Entstehung des Hydrocephalus internus. *Zts. f. d. ges. Neur. & Psychiat.*, 88: 208.

ZYLBERLAST-ZAND, N. 1924. Rôle protecteur de la pie-mère et des plexis choroides. *Rev. Neurol.*, 2: 235.

THE CHANGING CONCEPT OF OVARIAN RHYTHMS

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THE day is not in the far distant past when schools, medical as well as others, alike taught their students that all germ cells in the mammalian ovary were irrevocably formed during foetal life, and thereafter grew to maturity at stated times during adult life. Curiously enough, this static condition in the germ cells and germinal epithelium was not considered incompatible with what was recognized as regular rhythms in ovarian functional activities other than the production of germ cells. These were the regularly recurring oestrous periods in the lower mammals and menstrual cycles in the primates, with the maturation of follicles, ovulation, and the formation of corpora lutea. In other organs of the body also it was granted that the cells were constantly breaking down and being replaced by newly-forming ones, from which arose the popular idea that the body was renewed every seven years. Why the germ cells should be an exception so strikingly unlike other tissues of the body no one has attempted to explain.

When the amount of work that has been done on the mammalian ovary in the past twenty years is considered, it is truly remarkable that the actual facts concerning the production of germ cells should have received so little recognition among biologists. Yet it is a question of great biological as well as practical importance.

THE EVIDENCE FOR PERIODIC FORMATION OF GERM CELLS THROUGH ADULT LIFE

The modern attack on this problem may be said to have begun with the work of Arai in 1920, though he was not the first to suggest that there was a continuous formation of germ cells through adult life. Before this period there were many references to such a possibility, a tabular summary of which is given in table 1. These observations were made on a wide variety of mammals, including man, and indicate a striking uniformity in results. It is generally conceded that Pflüger (1863) was the first to describe the ingrowths of new cells from the germinal epithelium, the classical Pflüger's tubes, but he also believed that this new growth was periodic, recurring at each mating season. During the same year Schrön noted an increase in the number of young ova immediately beneath the germinal epithelium in cats and rabbits during oestrum and in the human during menstruation. This idea of a periodic production of new germ cells brought out by these investigators, lay in fallow ground until the work of Allen appeared in 1923, when he described a cyclical production of new germ cells during each oestrous cycle in the mouse.

In the earlier work the next important contribution was that of Paladino (1887, 1888, 1903). He studied a wide range of animals and concluded that there was a continual degeneration of both ova and follicles and continuous regeneration of these from the germinal epithelium throughout adult life. As we shall see later, these two conclusions, a degeneration and regeneration of ova and follicles from the germinal epithelium, with a periodic reformation of these, discovered by these early investigators, cover the essential facts brought out by the latest

TABLE 1

Tabular Summary of Literature on New Germ Cells Produced in Adult Life in Mammals

MAMMAL	AUTHOR	REMARKS
Bat	Van Beneden (1880)	Ova in germinal epithelium
Mouse	Harz (1883)	Ova in germinal epithelium
	Lange (1896)	Ova in germinal epithelium
	Allen (1923)	Ova in germinal epithelium
	Brambell (1927)	Ova produced rhythmically
Rat	Arai (1920)	For at least one year after birth
	Butcher (1927)	Ova from germinal epithelium
	Swezy (1929)	Continuous production of ova
	Hargitt (1930)	Continuous production of ova
	Evans and Swezy (1931b)	Rhythmical production of ova
Guinea pig	Harz (1883)	Ova in germinal epithelium
	Paladino (1888)	Continuous production of ova
	Papanicalaou (1924)	Continuous with varying intensity
	Evans and Swezy (1931b)	Rhythmical production of ova
Rabbit	Schrön (1863)	Increase in new ova at oestrum
	Coert (1898)	Ova in germinal epithelium
	Lane-Claypon (1905)	From interstitial cells
Ferret	Robinson (1918)	Development from germinal epithelium
Cat	Pflüger (1863)	Periodical ova from epithelial tubes
	Schrön (1863)	Increase in new ova at oestrum
	Harz (1883)	Ova in germinal epithelium
	Coert (1898)	Ova in germinal epithelium
	Evans and Swezy (1931b)	Rhythmical production of ova
Dog	Waldeyer (1870)	Cords from germinal epithelium
	Wagener (1879)	Epithelial thickenings
	Paladino (1888)	Continuous production of ova
	Evans and Swezy (1931b)	Rhythmical production of ova
Cow, Bear, Pig, Goat, Horse, Dolphin	Paladino (1888)	Continuous regeneration of ovary from germinal epithelium through adult life
Lemur	Rao (1927)	Epithelial cords and cells
Monkey	Evans and Swezy (1931b)	Rhythmical production of ova
Man	Schrön (1863)	Increase in new ova at menstruation
	Koster (1868)	Epithelial ingrowths
	Amann (1899)	Ova in germinal epithelium
	Paladino (1888)	Continual formation
	Fellner (1909)	Epithelial cords and single cells
	Evans and Swezy (1931b)	Rhythmical production of ova

studies on this material, though they have hitherto received but little recognition from biologists generally.

Other contributions through this period were fragmentary, though confirming the work already noted, describing the appearance of ova in the germinal epithelium and the ingrowth of epithelial cords from the germinal epithelium. With the work of Arai in 1920 a new attack on the problem was made. He counted the number of ova and follicles in the entire ovary of a number of rats at all ages and decided that ovogenesis was a continuous process. This was followed by the similar studies of Allen in 1923. His systematic study of a series of ovaries of mice through the entire oestrous cycle confirmed the conclusions of Pflüger and Schrön that there was a periodic formation of new germ cells. He found that mitoses in the germinal epithelium, which he considered preliminary to germ cell formation, were more numerous at oestrum than at other periods of the cycle, with an average of 400 to 500 new ova being formed in each oestrous cycle. This was followed by degeneration, only about one per cent of them surviving. Later (Allen, Kountz, and Francis, 1925), he found that the greater part of this degeneration took place among the follicles, where the ratio of degeneration was about 85 per cent.

These results were confirmed by Papanicalaou (1924) on the guinea pig, though he considered ovogenesis a continuous process which varied in intensity, being modified by seasonal conditions, but especially by an active corpus luteum. He concluded that follicles must grow or die; it was impossible for them to persist for any length of time. Like Allen, he found that only a few follicles survived to maturity.

Butcher (1927) studied the immature and adult rat, finding that ovogenesis was a continuous process but adding no new information as to its periodicity. This was further confirmed by Swezy (1929) and Hargitt (1930). The latter author discussed the probability of a periodic formation of new germ cells but was inclined to believe this was a continuous process in this animal.

The studies of Evans and Swezy (1931b) extended the work of these investigators both intensively and extensively. It was shown that ovogenesis occurred throughout adult life in the rat, guinea pig, dog, cat, monkey, and man, by outgrowths from the germinal epithelium, either as single cells or as epithelial cords. It was also shown that this production of new germ cells was a rhythmical process, closely related to the ovarian rhythms characterized by maturation of the follicles, ovulation, and the formation of the corpora lutea. During the middle of the ovulation or ovarian cycle, metoestrum and anoestrum in the lower mammals, there was an extensive proliferation of new germ cells from the germinal epithelium, with the growth of many small and medium sized follicles, along with regression of the corpora. Towards the end of the cycle, at the time of ovulation, there was a drop in the production of new germ cells and a slowing up of follicular growth, with atresia of all follicles which did not ovulate. The beginning of the new cycle was marked, a short time after ovulation had occurred, by a resumption of growth, both in the production of new ova from the germinal epithelium and in the growth of small and medium sized follicles. These alternate phases of growth and regression take place in each ovarian cycle. The dictum of Papanicalaou that all follicles must grow or die was extended by showing that the germ cells, far from being long lived, probably have the shortest life span of any group of cells in the body.

Animals with a short cycle, as the rat and mouse, form the most unfavorable material for these investigations, since the length of time necessary for complete growth of follicles, as well as complete atresia, is so near the entire length of the oestrous cycle that these relations are obscured. The guinea pig, with its cycle of about sixteen days, is one of the best for this purpose, the ovary showing clear cut pictures for each phase of the cycle.

It is thus seen that a fairly large number of mammals have been recorded as showing evidences of the cyclical formation of ova and follicles throughout adult life. In a still greater number it has been shown that ovogenesis occurs during adult life, the lack of serial study of ovaries of many individuals obscuring the periodic relationships. The wide variety of animals which have been used strongly suggests that these conclusions are applicable to the Mammalia generally.

EVIDENCE AGAINST PERIODIC FORMATION OF GERM CELLS

An equally large number of investigators, working on the same animals, found no evidences of such new formations of germ cells during adult life, though large cells in the germinal epithelium were noted in most cases. One stumbling block to the recognition of these cells as germ cells has been the lack of maturation phases in the formation of chromosomes, as reported by Cowperthwaite (1925), and others. It has been definitely shown by Kingery (1917), Allen (1923), Brambell (1927), Swezy (1929), Hargitt (1930), and Evans and Swezy (1931b) that such phases do not occur in the definitive ova in mammals which have been carefully investigated.

Others, as Kingsbury (1913), felt that an attempt to explain the presence of these cells was unnecessary, and Waldeyer, though finding new germ cells in adult dogs in his earlier studies (1870), in his later paper (1906) states his belief that ovogenesis does not occur in the adult, though admitting a prejudice by saying that the establishment of this concept would controvert Weissmann's theory, which he believed.

PROLIFERATION AND DEGENERATION OF OVARIAN TISSUES

The components of the ovary may be divided into two main divisions, the fundamental structures and the generative portion, the former composed of stroma, connective tissue, blood vessels, etc., and the latter of germinal epithelium, tunica albuginea, germ cells, interstitial cells, follicles, and corpora. The rhythms of ovarian functioning are participated in, to some extent, by the first group, but it is the generative portion of the ovary which produces the striking changes noted at oestrum and anoestrum. In the formation of follicles and corpora the connective tissue and blood vessels play a part, these tissues thus having a proliferative phase, followed by a degeneration of the new tissue thus formed, coextensive with the phases of growth and regression of the follicles and corpora. In the generative portion the amount of new germ cell and follicular tissue thus formed in each cycle is enormous, and an equal amount of degeneration takes place in each cycle. This may readily be seen by comparing the pictures presented by the ovary at anoestrum with that at oestrum, particularly in the dog and guinea pig (Evans and Swezy, 1931b). These ovarian rhythms are not confined to the maturation of follicles, ovulation, and corpora formation, as was commonly supposed, but include a proliferation of new germ cells, and furthermore, extend to the fundamental structures of the ovary itself, periodical growth, followed by degenera-

tion and absorption of the tissues thus formed, being found throughout the entire organ. As was first pointed out by Paladino (1888), the germinal epithelium is the important factor in this periodic regeneration of these ovarian structures, from it arising ova, follicles, corpora lutea, and interstitial cells. It is thus the fundamental basis from which arise all ovarian changes.

THE RELATION OF OESTRUS AND MENSTRUATION TO OVULATION

The regular recurrence of oestrous periods in the lower mammals and menstruation in the primates has long been a matter of common knowledge, but it remained for investigators in recent years to show that these external manifestations were connected with an equally regular recurrence of certain events in the ovary. A review of the literature on this question is outside of the scope of this paper, an ample discussion of the earlier work being found in Marshall (1922). In those of the lower mammals which have regular cycles, it has been found that ovulation takes place at a time which can be predicted in a fairly definite manner (Stockard and Papanicalaou, 1917; Long and Evans, 1922). This fact has become the basis of most of the experimental work on the interrelations between the gonads and their controlling hormones. So close is this relation between the oestrous cycles and the ovarian cycles in these animals that the period of the oestrous cycle can be determined with a high degree of accuracy by an examination of the ovary. This is important in that it indicates that the length of each phase of the ovary is fairly stable in a given species or strain, under normal conditions, with an adequate food supply. Thus, in the guinea pig (Loeb, 1911; Evans and Swezy, 1931b), the tenth to the twelfth days of the oestrous cycle will invariably show the presence of many follicles in the ovary, with the first evidences of regression in the corpora lutea, while prooestrum will show much follicular atresia, along with a few maturing follicles. Anoestrum in the opossum (Hartman, 1923) is always accompanied by the presence of great numbers of follicles, most of which are atretic. In the pig (Allen, Kountz, and Francis, 1923), macroscopic examination is sufficient to determine the approximate period of the oestrous cycle, follicles of three to six millimeters in size not being present before about the eleventh day and larger than these from about the fifteenth day, with a complete disappearance of all visible follicles after ovulation. The work of Allen, Pratt, Newell, and Bland (1930) on the human ovary shows the same periodicity. In their descriptions of 35 ovaries, they show that follicles less than seven millimeters were present in four, follicles between seven and ten millimeters in seventeen, and fourteen contained follicles larger than ten millimeters, this size being considered an ovulation size. Comparing these data with those given for the pig and the lower mammals, it is evident that the first group, with only small follicles, was near the beginning of the ovarian cycle, the second group, with follicles from medium up to ovulation size, was at the middle up to the preovulation period, and the third group at the ovulation period. The total lack of any recognizable relation between these ovarian phases and the periods of the menstrual cycle at which they were found agrees with the conclusions noted below. The ovaries with only small follicles were found at days twelve, sixteen, seventeen, and twenty-two, those with follicles of ovulation size occurred at days two, eight, nine, and up to twenty-three, and medium sized follicles at all dates from the second to the twenty-third.

Long continued observation of single individuals by a number of investigators produces evidences that, while the length of the oestrous cycle may vary from individual to individual of a species or race or even a particular strain, yet it tends to be fairly regular in a single individual, each seeming to have its own special rhythm. There is some evidence that these cycles have less tendency to great variation in larger animals than in the smaller ones, such as the rat and mouse, under laboratory conditions. This seems to apply equally well to the ovarian phases which accompany these cycles.

In animals like the cat, where there is no necessary correspondence between the ovarian phases and the oestrous cycles (Evans and Swezy, 1931b), this lack seems to be only in the oestrous cycles, which are irregular, varying from a few days to two months or more in length, while the ovarian cycle exhibits the same regularity noted in other animals, with a periodicity of about seventy-five days. In the primates also there is no exact correspondence between the ovarian cycles and the menstrual cycles (shown in the data given by Schröder, 1930, though not in his conclusions, and in the work of Allen *et al.*, cited above, among others), though each seems to have the same periodicity of about twenty-eight days. Even with this lack of synchronism, however, all the evidence points to a regular rhythm in their occurrence, a rhythm which seems to be as fundamental in the primates as in the lower mammals, with the same manifestations of alternate growth and regression in all of the components of the ovary, with its associated growth and regression in the uterus. This rhythm, as we will show, is dependent on the reactions between certain hormones (Moore and Price, 1932; Evans and Swezy, 1933), and, since these hormones are alike in all mammals, it is to be expected that the functional changes resulting from them would be similar.

Considerable discussion has taken place around the question of the relation of the ovulation cycle to the menstrual cycle, and the statement made above is by no means generally accepted; yet, when all the facts are considered in connection with this fundamental importance of regular rhythms in both morphology and physiology in the ovary, with the data given by many investigators, including the dissenters, no other conclusion seems tenable. It has been shown (Evans and Swezy, 1931a) that the available data, gathered from many sources, clearly indicate that ovulation may take place at any time in the menstrual cycle, though tending to occur more frequently during the middle third of the cycle. Some investigators maintain that it can occur only at the mid-interval period, though Allen *et al.* have shown that follicles of ovulation size may be found at all periods ranging from day two to twenty-three, as noted above.

It was first shown by Sutton (1886) that menstruation may occur without corpora in the ovary of the monkey, with a low interval type of uterus. Other early investigators (De Sinety, 1881; Heape, 1897; Möriche, 1882; Lipes, 1904; Oliver, 1906, 1907) had indicated the same thing. This was fully confirmed by the later work of Corner (1927), Allen (1926), and Hartman (1927). This fact, so contrary to the generally accepted view, in itself is good proof that menstruation is independent of both ovulation and corpora formation, and hence seems to invalidate the idea of a close relation between the two cycles, and particularly the idea that the regression of the corpus is related to the appearance of the following menstrual period. The latter assumption seems to rest mainly on theoretical grounds, all of which are contradicted by the evidence

just cited. There are no exact data indicating how long the corpus is functional but the consensus of opinion seems to be that it is about ten days. Since ovulation occurs more frequently during the middle third of the cycle, this results in the more frequent appearance of regressing corpora near the time of menstruation than corpora in other phases. There is evidence that they occur at other times also.

In investigating the relation between ovulation and the menstrual cycle, the greatest emphasis has been placed on the finding of tubal eggs, both in the human and in the monkey. The dates on which these have been reported range from the tenth to the nineteenth day of the menstrual cycle. In his most recent summary of work on the monkey, Hartman (1932) reports "111 accurately determined ovulation days," his data being derived from gynecological evidence, time of conception, and ovulation as determined by palpation. These days range from the ninth to the twentieth day of the menstrual cycle. In an earlier paper Hartman (1929) concludes that the midinterval bleeding in primates occurs as a result of the congestion following ovulation. The range of time during which this has appeared in his monkeys he gives as the seventh to the eighteenth day. Adding these to the list given above, the range of time during which ovulation has apparently occurred in these primates extends from the seventh to the twentieth day of a twenty-eight day cycle. It must be further noted that more animals have been examined during the middle of the cycle than at other periods. The range of variation shown in these results is so great that it is at once evident that we must discard the idea that ovarian function is fundamentally rhythmical, or else discard the idea that there is a fixed relation between the ovarian and the menstrual cycles. It may be questioned whether the average or mean time has any value in judging this relationship. If the two cycles are definitely related the variation in the one should correspond to the variation in the other and this is not the case, as may be seen in Schröder's tabulation.

The menstrual cycle is remarkable in its regularity. In the cases under discussion the cycles were regular in some instances. If we consider the regression of the corpora related to the following menstruation, we must believe that the corpora in these cases had a functional life span varying from eight to twenty-one days. Our knowledge of the regularity of the menstrual cycle and the regularity of the oestrous and ovarian cycles in the lower mammals at once leads us to cast out this as a working hypothesis. It seems fairly certain that the corpora formed at day nine will regress in approximately the same time as those formed at day twenty, in which case the menstrual period will show corpora in advanced stages of regression. That the menstrual period does coincide with all stages of regression and growth of the corpora is amply proven by Schröder's (1930) careful examination of portions of uteri from 898 human cases, the uterus being an accurate criterion of the phase of development of the corpus. So far as the facts go, there is no evidence that the ovarian cycle in the primates is more erratic than is the menstrual cycle, or the cycles of the lower mammals, a theory we must accept if we consider the two cycles as having a necessary time relation. All the evidence in the lower mammals indicates that these periods are relatively stable in most species. Neither is there any valid evidence that these processes are radically different in the primates from those prevalent in the lower mammals. This is true in the morphology of the ovary (Evans

and Swezy, 1931b), as well as in the results obtained by the response of monkeys to the experimental administration of hormones (Hartman and Squier, 1931; Smith and Engle, 1932; and others).

Closely paralleling these changes in the ovary, it has been shown that the uterus also functions in cycles as regular as those of the ovary, its period of greatest development coinciding with the ovulation period and the functional life of the corpus, and its regression with the first beginnings of regression in the corpus. This has been most convincingly demonstrated by Schröder (1928) in the human, Loeb (1911) and Stockard and Papanicalaou (1917) in the guinea pig, Corner (1921) in the sow, Long and Evans (1922) in the rat, among others. In the earlier work that of Heape (1900) stands as an important landmark. In addition to these morphological contributions, much experimental work by many investigators proves, beyond a doubt, that these uterine cycles are intimately bound up with the ovarian cycles of follicular growth and maturation and corpus formation and regression, the hormone secreted by the follicles causing early growth and the progestin from the corpora continuing its fullest development. So close is this relation that, as we have pointed out in an earlier paper (Evans and Swezy, 1931a), a study of the uterus gives more reliable information concerning the phase of the ovarian cycle than does a study of the ovary itself. This is especially true of the corpora, since regression in the uterus will be evident before the corpus shows marked indications of it, the change in hormone production being a more delicate test than morphological changes and seeming to occur earlier. In animals where ovulation may not occur without copulation, as in the cat, the only reliable test of the presence of the ovulation period is found in the degree of development of the uterus, a certain amount of growth always occurring before ovulation. When the mature follicles degenerate without ovulation, immediate regression of this new growth takes place in the uterus (Evans and Swezy, 1931a), with an earlier reversion to the low interval type of structure than is found when a corpus is present. Definite cycles occur with or without an accompanying ovulation, the amount of growth attained by the uterus and the length of time after the ovulation period before it begins to regress, being the only apparent differences between them.

In the great amount of experimental work that has been done (Leonard *et al.* 1932, and others), showing that the folliculin present near the end of the growth phase in the ovary is the stimulus for the development of the uterus, followed by other definite changes with the production of progestin by the corpus, ample evidence is given that these morphological changes in the ovary are accompanied by physiological changes that are equally profound. It is these physiological results which give to the functional rhythms of the ovary their importance.

THE ENDOCRINE MECHANISM OF THE CYCLE

This hastily drawn picture of the closely interwoven rhythms of growth and regression in the ovary and uterus, compounded of both morphological and physiological changes closely associated with external manifestations of oestrum in the lower mammals, would not be complete without some attempt to specify the mechanism which keeps the wheels going round. Fortunately the extensive as well as intensive work that has been occupying the time and attention of many investigators on hormones and their relations to the gonads, offers this explanation, incomplete though it is. So extensive has the literature on this subject become that

any attempt to give an adequate survey of it in a short paper is hopeless. The outstanding results only can be indicated.

Studies on the hypophysectomized rat (Smith, 1927, 1930) have shown, beyond a doubt, that the follicular-growth hormone of the anterior pituitary is the stimulus for the growth of follicles beyond a small size. A considerable amount of experimental work (Leonard, Meyer, and Hisaw, 1931, among others) also demonstrates the fact that the sex hormone of the ovary, or the folliculin secreted by the follicles which have reached a certain maturity is antagonistic to the hormones of the anterior pituitary, and, when present in amounts equal to that found in mature follicles, suppresses them, with a consequent lack of further growth in the follicles. Referring back to what has been said concerning the ovarian cycles in normal animals, it is found that the middle of the cycle sees the growth of many follicles, which must be due to the follicular-growth hormone, and that at the end of the cycle, when mature follicles are present, all of the follicles disappear, either through ovulation or atresia. This stoppage of follicular growth must be due to a cessation of output of the follicular-growth hormone by the anterior pituitary, and is evidently caused by the suppression of this function by the folliculin which has been produced in the ovary. The mature follicles thus form the agent by means of which the formation of the hormone upon which their own growth and well-being depend is suppressed, resulting in an almost total lack of growth at this period and atresia of all follicles already present. This, in turn, results in a drop in the amount of folliculin present, thus allowing the anterior pituitary to renew the production of follicular-growth hormone, starting a new cycle of growth in the ovary. The interaction of these two hormones, the follicular-growth hormone of the anterior pituitary and folliculin from the ovary, thus forms a self-regulating mechanism by means of which the physiological and morphological rhythms of the ovary and uterus are produced and maintained throughout adult life. This has been worked out in great detail by Moore and Price (1932) from the experimental side, and summarized for the normal animal by Evans and Swezy (1933).

With the suppression of the follicular-growth hormone, the luteinizing hormone of the anterior pituitary becomes active, with ovulation followed by the formation of corpora lutea. It seems quite probable that ovulation is caused by some other factor than the luteinizing hormone, but in the normal cycle these are not clearly separated.

Recent investigations (Swezy, 1933) show that the luteinizing hormone of the anterior pituitary has a depressing effect on the production of new germ cells in the ovaries of rats when this is given under experimental conditions. During the normal cycle this effect is shown by the lowering of the rate of ovogenesis at the time of ovulation when this hormone is acting in the ovary. The follicular-growth hormone seems to have less of this effect, hence the appearance of great numbers of new germ cells during the middle of the cycle when the greatest amount of follicular growth occurs. The results of the experimental administration of these hormones is thus confirmed by the conditions found during the ovarian cycle in the normal animal.

After an operative removal of the anterior pituitary (Smith, 1927; Swezy, 1933), which brings about an entire absence of all of these hormones, there is an entire absence of all rhythms in the ovary, with profound atrophy of the uterus. Atrophy

in the ovary is less complete, and is characterized by the absence of all medium and large sized follicles and corpora, the production of new germ cells continuing at an increased rate. Ovogenesis seems to be a continuous process after this operation with continuous degeneration among the ova, thus confirming the relation indicated between the hypophysial hormones and this process in the normal animal, as in the experimental animals which have received these hormones.

LIST OF LITERATURE

ALLEN, E. 1923. Ovogenesis during sexual maturity. *Amer. Jour. Anat.*, vol. 31, pp. 439–482.

———. 1926. The time of ovulation in the menstrual cycle of the monkey, *Macacus rhesus*. *Proc. Soc. Exp. Biol. Med.*, vol. 23, p. 381.

———. 1928. Reactions of immature monkeys to injections of ovarian hormone. *Jour. Morph. and Physiol.*, vol. 46, pp. 479–519.

ALLEN, E., KOUNTZ, W. B., and FRANCIS, B. F. 1925. Selective elimination of ova in the adult ovary. *Amer. Jour. Anat.*, vol. 34, pp. 445–468.

ALLEN, E., PRATT, J. P., NEWELL, Q. U., and BRAND, L. J. 1930. Human ova from large follicles; including a search for maturation divisions and observations on atresia. *Amer. Jour. Anat.*, vol. 46, pp. 1–54.

AMANN, J. A. 1899. Ueber Bildung von Ureiern und primärfollikelähnlicher Gebilde im senilen Ovarium. *Fest. f. Kupffer*, pp. 717–730.

ARAI, H. 1920. On the postnatal development of the ovary (albino rat), with especial reference to the number of ova. *Amer. Jour. Anat.*, vol. 27, pp. 405–462.

BRAMBELL, F. W. R. 1927. The development and morphology of the gonads of the mouse. I. The morphogenesis of the indifferent gonad and the ovary. *Proc. Roy. Soc.*, B, vol. 101; pp. 29–56.

BUTCHER, E. O. 1927. The origin of definitive ova of the white rat. *Anat. Rec.*, vol. 37, pp. 13–30.

COERT, H. J. 1898. Over de ontwikeling en den bouw van den geslachtsklier bijde zoogdiern meer in het bijzonder van den eirstock. Akad. Proefschrift, *Leiden*.

CORNER, G. W. 1921. Cyclic changes in the ovaries and uterus of the sow and their relation to the mechanism of implantation. *Carnegie Cont. Embryol.*, vol. 13, pp. 117–146.

———. 1927. The relation between menstruation and ovulation in the monkey: its possible significance in man. *Jour. Amer. Med. Assoc.*, vol. 89, pp. 1838–1840.

COWPERTHWAITE, M. H. 1925. Observations of pre- and postpubertal ovogenesis in the white rat *Mus norvegicus albinus*. *Amer. Jour. Anat.*, vol. 36, pp. 69–90.

DE SINETY. 1881. Recherches sur la muqueuse utérine pendant la menstruation. *Annal. de Gynaec.*, vol. 15, pp. 295–296.

EVANS, H. M., and SWEZY, O. 1931a. The uterus-ovary relationship and its bearing on the time of ovulation in primates. *Amer. Jour. Physiol.*, vol. 96, pp. 628–639.

———. 1931b. Ovogenesis and the normal follicular cycle in adult mammalia. *Mem. Univ. Calif.*, vol. 9, pp. 119–224.

———. 1933. On hypophysis-ovary relationships as the cause of female sex rhythm. In press.

FELLNER, O. O. 1909. Histologie des Ovariums in der Schwangerschaft. *Arch. mikr. Anat.*, vol. 73, pp. 288–305.

HARGITT, G. T. 1930. The formation of the sex glands and germ cells of mammals. III. The history of the female germ cells in the albino rat to the time of sexual maturity. *Jour. Morph. Physiol.*, vol. 49, pp. 277–331.

HARTMAN, C. G. 1923. The oestrous cycle in the opossum. *Amer. Jour. Anat.*, vol. 33, pp. 353–421.

———. 1927. Menstruation without ovulation in *Macacus rhesus:* an account of an experiment. *Anat. Rec.*, vol. 35, p. 13.

———. 1929. The homology of menstruation: new observations of intermenstrual bleeding in the monkey. *Jour. Amer. Med. Assoc.*, vol. 92, pp. 1992–1993.

———. 1932. The time of ovulation in the menstrual cycle. *Anat. Rec.*, vol. 52, p. 14.

HARTMAN, C. G., and SQUIER, R. R. 1931. The follicle-stimulating effect of pig anterior lobe on the monkey. *Anat. Rec.*, vol. 50, pp. 267–274.

HARZ, W. 1883. Beiträge zur Histologie des Ovariums der Säugetiere. *Arch. mikr. Anat.*, vol. 22, pp. 374–407.

HEAPE, W. 1897. The menstruation and ovulation of *Macacus rhesus*, with observations on the change undergone by the discharged follicle. *Phil. Trans. Roy. Soc. London*, B, vol. 76, pp. 135–166.

———. 1900. The "sexual season" of mammals and the relation of "pro-oestrum" to menstruation. *Quart. Jour. Micr. Sci.*, vol. 44, pp. 1–70.

KINGERY, H. M. 1917. Ovogenesis in the white mouse. *Jour. Morph.*, vol. 30, pp. 261–315.

KINGSBURY, B. F. 1913. The morphogenesis of the mammalian ovary: *Felis domestica*. *Amer. Jour. Anat.*, vol. 15, pp. 345–387.

LANE-CLAYPON, J. E. 1905. On the origin and life history of the interstitial cells of the ovary of the rabbit. *Proc. Roy. Soc. London*, B, vol. 77, pp. 32–57.

LANGE, J. 1896. Die Bildung der Eier und der Graaf'schen Follikel bei der Maus. *Verh. phys. med. Gesell. Würzburg*, N. F., vol. 30, pp. 57–74.

LEONARD, S. L., MEYER, R. K., and HISAW, F. L. 1931. The effects of oestrin on the development of the ovary in immature female rats. *Endocrin.*, vol. 15, pp. 17–24.

LIPES, H. G. 1904. A study of the changes occurring in the endometrium during the menstrual cycle. *Albany Med. Annals*, vol. 94, pp. 94–105.

LOEB, L. 1911. The cyclic changes in the ovary of the guinea pig. *Jour. Morph.*, vol. 22, pp. 37–70.

LONG, J. A., and EVANS, H. M. 1922. The oestrous cycle in the rat and its associated phenomena. *Mem. Univ. Calif.*, vol. 6, pp. 1–148.

MARSHALL, F. H. A. 1922. The Physiology of Reproduction. *London*, Longmans, Green and Co.

MOERICKE, R. 1882. Die Uterusschleimhaut in den verschiedenen Altersperioden und zur Zeit der Menstruation. *Zeit. f. Geburt. u. Gynaek.*, vol. 7, pp. 84–137.

MOORE, C. R., and PRICE, D. 1932. Gonad function, and the reciprocal influence between gonads and hypophysis with its bearing on the problem of sex antagonism. *Amer. Jour. Anat.*, vol. 50, pp. 13–72.

OLIVER, J. 1906. Gleanings concerning menstruation. *N. Y. Med. Jour.*, vol. 84, pp. 270–273.

———. 1907. A further contribution concerning menstruation. *N. Y. Med. Jour.*, vol. 85, pp. 1177–1178.

PALADINO, G. 1888. La destruction et le renouvellement continuel du parenchyme ovarique des mammifères. *Arch. Ital. de Biol.*, vol. 9, pp. 176–202.

PAPANICALAOU, G. N. 1924. Ovogenesis during sexual maturity as elucidated by experimental methods. *Proc. Soc. Exp. Biol. Med.*, vol. 21, pp. 393–396.

PFLÜGER, F. 1863. Die Eierstocke der Säugetiere und der Menschen. *Leipzig.*

RAO, C. R. N. 1927. On the structure of the ovary and the ovarian ova of *Lorica lydekkerianus* Cabr. *Quart. Jour. Micr. Sci.*, vol. 71, pp. 57–74.

ROBINSON, A. 1918. On the formation, rupture, and closure of ovarian follicles in ferrets and ferret-polecat hybrids, and some associated phenomena. *Proc. Roy. Soc. Edin.*, vol. 52, pp. 303–362.

SCHRÖDER, R. 1930. Die weibliche Genitalorgane. *Handb. mikr. Anat. der Menschen*, vol. 7, pp. 329–556.

SCHRÖN, O. 1863. Beitrag zur Kentniss der Anatomie und Physiologie des Eierstockes der Säugethiere. *Zeit. f. wiss. Zool.*, vol. 12, pp. 409–426.

SMITH, P. E. 1927. The disabilities caused by hypophysectomy and their repair. *Jour. Amer. Med. Assoc.*, vol. 88, pp. 158–161.

———. 1930. Hypophysectomy and a replacement therapy in the rat. *Anat. Rec.*, vol. 45, pp. 205–274.

SMITH, P. E., and ENGLE, E. T. 1932. Prevention of experimental bleeding in *Macacus* monkey by corpus luteum extract. *Proc. Soc. Exp. Biol. Med.*, vol. 29, pp. 1225–1227.

STOCKARD, C. R., and PAPANICALAOU, G. N. 1917. The existence of a typical oestrous cycle in the guinea pig—with a study of its histological and physiological changes. *Amer. Jour. Anat.*, vol. 22, pp. 225–284.

SUTTON, B. 1886. Menstruation in monkeys. *Brit. Gynaec. Jour.*, vol. 2, pp. 285–292.

SWEZY, O. 1929. The ovarian chromosome cycle in a mixed rat strain. *Jour. Morph. and Physiol.*, vol. 48, pp. 445–473.

———. 1933. Ovogenesis and the Hypophysis: the Effects of Pregnancy, Hypophysectomy, Thyroidectomy, and Hormone Administration on the Ovary of the Rat. The Science Press.

VAN BENEDEN, E. 1880. Contribution à la connaissance de l'ovaire des mammifères. *Arch. de Biol.*, vol. 1, pp. 475–550.

WAGENER, G. 1879. Bemerkungen über den Eierstock und den gelben Körper. *Arch. f. Anat. u. Phys.*, 175–200.

WALDEYER, W. 1870. Eierstock und Ei. *Leipzig.*

———. 1906. Die Geschlechtzellen. *In* "Handbuch der vergleichen. u. exp. Entwickelung. der Wirbeltiere," O. Hertwig.

MORPHOGENESIS OF THE SHOULDER ARCHITECTURE
PART II. PISCES

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HISTORICAL

MACLISE (1832) and Oken (1843) looked upon the limb girdles in the light of modified ribs. Owen was of the same opinion, but in addition he believed that the limb bones are homologous to such structures as the uncinate processes of the ribs of birds and branchiostegal rays. It was not, however, until after the middle of the century that the girdles came in for the share of attention which they merit. At this time Gegenbaur (1865) advanced the belief that not only the pectoral but the pelvic arch as well have developed from gill arches, the bones of the limbs proper representing gill rays. Davidoff, Fürbringer, Braus and others have held the same opinion. Parker, in various papers, has stated his belief that the pectoral girdle represents an extrabranchial cartilage—a more plausible contention. But the thesis that the appendages are derived from essentially branchial elements has never enjoyed the popularity of the so-called finfold theory, holding that the paired as well as the unpaired fins represent local remnants of continuous longitudinal fins. This theory was advanced independently and almost simultaneously by Thacher (1877), Balfour (1878), and Mivart (1879). In its essential features it has been accepted also by Haswell (1883), Dohrn (1884), Mayer, Wiedersheim (1892), Mollier (1893), Woodward, Harrison (1895), Dean (1896), Rabl (1901), Regan (1904), Goodrich (1906), Osburn (1907), Sewertzoff (1907) and many others. Many of the investigators on the subject, however, have failed properly to commit themselves whether they considered that the paired fins have had endo- or exoskeletal derivation. Among those who have definitely subscribed to nonaxial derivation have been Mivart, Cuvier, Huxley, Silliman; while Goodsir (1857), Macalister (1877), G. St. Hilaire, and Gregory believed that the fins have had a nonaxial or peripheral origin.

The theories of fin genesis will be further considered in future chapters.

APINNATE CHORDATES

It is desirable to call brief attention to the lancelet and cyclostomes because of the arrangement of their nerves and myomeres. Both are more highly specialized than is usually admitted. In *Amphioxus* there are dorsal myotomes with a basic appearance, for they are segmented and staggered diagonally, but the facts that ventral muscle fibers run transversely rather than axially and that these are innervated by the dorsal rami of the spinal nerves are utterly divergent from the vertebrate plan. The lack of a brain, the anterior extension of the notochord, and the presence of the atrium are further divergent features.

The Cyclostomata are, of course, very primitive in most respects and are thus useful in comparative anatomy, but they are very clearly degenerate and almost parasitical. Allen (1917) investigated the

spinal nerves of *Polistotrema* and found them basically primitive in that the dorsal sensory and dorsal motor branches are separate. This is true as well in the case of the more caudal of the ventral branches, but those more anteriorly have fused. In embryos of *Squalus* most of the sensory and motor nerves are separate also, and fusion takes place by peripheral union, this then progressing centrally.

FOSSIL PREFISHES

The known forms may be briefly considered in four groups as follows:

I. Paleospondyli, apinnate and of doubtful affinities.

II. Ostracodermi. Silurian and Devonian ostracoderms were the oldest known chordates (Gregory, 1915). The same author (1933) considers that ostracoderms as a class were the archetypal vertebrates from which were derived cyclostomes on the one hand, and gnathostomes on the other, but such a common ancestor must have been much more generalized than any ostracoderm yet discovered. Of the three orders the Heterostraci, apodial so far as known, may be excluded from consideration because the exoskeleton was of dentine rather than of bone. In the Osteostraci the exoskeleton was largely of bone. In the only family that is well known, the Cephalaspidae, there was an extensive cephalic shield and at least in some sorts there was a pair of anterior appendages, which, however, may not have been homologous to the pectorals of higher forms. Little is known of the shoulder architecture, but the limbs were probably used for the purpose of propulsion along the bottom by alternate action, and possibly for stirring up the mud in search of food. This would have involved antero-posterior rather than vertical movement of the limbs, and protractor-retractor musculature doubtless occurred. Additional details of Cephalaspids are mentioned in future chapters.

The third order usually considered as comprising the ostracoderms is the Anaspida, so grouped largely because there is no better position in which to place them. They were largely fish-like in form but appear to have been without paired appendages; and they had interesting, longitudinal rows of dermal scutes, ventrally placed, suggestive of similar structures in the sturgeon.

III. Antiarchi. This is an aberrant, highly specialized group, with a greatly developed, carapace-like shield of bony elements. There were club-shaped, anterior appendages but it is not known if these were strictly homologous with pectoral limbs. A group of high tangential specialization.

IV. Arthrodira. This group, with extensive joint between the shields of the cephalic and body regions proper, is of interest chiefly because some of its members appear to have had paired pelvic but no pectoral appendages.

The development of the tail in these prefishes is in a heterocercal direction, clearly indicating a bottom habitat. Some are without paired fins, in others there are pelvics, and in still others a pair which appears to correspond with pectorals, but in no sort known were both pairs present.

CHONDRICHTHYES

This group comprises the Elasmobranchii only, which may be divided into five orders (Bridge, 1922) as follows:

1. Acanthodei (extinct), comprising the acanthodians;
2. Pleuropterygii (extinct), including the cladoselachians;
3. Ichthyotomi (extinct), including the pleuracanthids;

4. Plagiostomi, including the sharks, Selachii, and rays and skates, Batoidei;
5. Holocephali, comprising the chimaeras.

Of these five the acanthodians occupy a pivotal position. Like so many other fossils the known forms are entirely too specialized to have occupied a directly ancestral position. Earlier, generalized members of the group may well have given rise to both the cartilaginous and bony fishes, although Bridge (1922) considered that the presence of shagreen tubercles indicated that they constitute a terminal offshoot of early elasmobranchs. At any

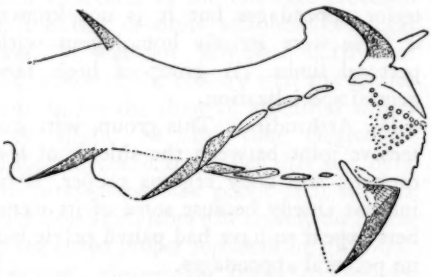

FIG. 5. APPENDAGEOUS STRUCTURES OF THE ACANTHODIAN PAREXUS FALCATUS, IN TWISTED POSITION AS FOUND: MODIFIED FROM DEAN

rate they appeared in late Silurian times, gave rise in the Devonian to a highly varied assortment of forms and disappeared at the close of the Permian. The rows of dermal protuberances which some of them had are extremely significant. Thus, Dean (1907) figured and described the interesting genus *Parexus* (fig. 5), in which there was a row of heavy dermal spikes along (clearly) the branchiocloacal line. The anterior of these is greatly hypertrophied, with the posterior only slightly less so, and posterior from each there appears to have been a fin membrane. In this genus, as in others, there is thus dermal evidence of a true pectoral and a true pelvic fin, separated by a hiatus. In *Acanthodes wardi*, however, (fig. 6) there were no true pelvic fins, the second pair clearly having been directly in posterior sequence with the pectorals, as in so many living teleosts. So this group apparently elaborated fins of different sorts out of paired series of longitudinal dermal structures.

All Elasmobranchii, other than acanthodians, had both pectoral and pelvic (as opposed to ventral) fins. The pleurocanthids are not of great interest in the present connection. Cladoselachians are

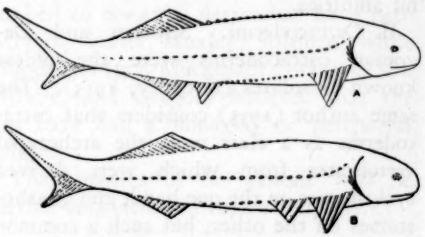

FIG. 6. HYPOTHETICAL RECONSTRUCTION OF TWO ANCESTRAL TYPES OF ACANTHODIANS, WITH LONGITUDINAL SERIES OF DERMAL STRUCTURES IN CRITICAL AREAS: (A) SHOWING EARLY DEVELOPMENT OF PECTORAL AND PELVIC FINS; (B) BASED ON ACTUAL CONDITIONS IN ACANTHODUS WARDI, WITHOUT PELVICS, BUT WITH DERIVATION OF VENTRAL FINS FROM THE POSTERIOR PART OF THE PECTORAL ELEMENT

the only certain representatives of the Pleuropterygii and are of particular interest because their fins have often been considered of extremely primitive type, chiefly because the radialia are relatively unconcentrated. As a matter of fact the fins appear to be much specialized, but in a manner that is unique among known forms.

The Selachii, or sharks, although exceedingly primitive in many respects, are far off the direct pathway that led to higher vertebrates. The exoskeleton is well developed but in a direction different from that taken by the direct line of

ascent, for the elements are discrete and occur in single dermal tubercles or placoid scales (shagreen) all over the body. Hence there are no membranous bones associated with endoskeletal cartilages, as must have been the generalized situation. The endoskeleton, too, with its slight calcification, exhibits a retrograde condition. Certain details of the muscles and particularly of the nerves of the more generalized sorts offer much evidence of significance, however, and these details are discussed elsewhere.

OSTEICHTHYES

This group contains all fish except the Elasmobranchii. No arrangement yet proposed is satisfactory in all respects, but the following may be used for the present:

Subclass Dipnoi—the lung fishes
Subclass Teleostomi
Division Crossopterygii—lobe-finned ganoids
Chondrostei—sturgeons and paddle fish
Holostei—gars and bowfins
Teleostei—true bony fishes

All the Osteichthyes have one character which is shared by the higher vertebrates and which is lacking in elasmobranchs, and that is the presence about the head of exoskeletal membranous plates which have become a structural part of the skeletal plan. Some of these are so arranged as to enclose the external gill aperture in a bony framework, and the posterior border of this forms a support for the developing endoskeletal structures. This, constituting the clavicular girdle, may maintain its original position largely at the surface of the body (sturgeon) but more often sinks beneath the surface, being grossly indistinguishable in the adult from bones of endoskeletal origin.

Dipnoans are in some respects very primitive, but in others, as the anatomy of the paired fins, dentition, and bones of the skull, they are highly specialized, and in a direction away from the main line of vertebrate ascent. It is likely that they arose from some of the more specialized crossopterygians (Regan, 1904). Of this group *Ceratodus* and *Protopterus* were dissected in the present connection.

The first three divisions of Teleostomi, consisting of Crossopterygii, Chondrostei, and Holostei, comprise the ganoids, and of them the second group is the most generalized in many respects, though not in all. Ganoids, like dipnoans, have both pectoral and true pelvic fins. *Polypterus* of the first group, *Acipenser* of the second, and *Amia* of the third were dissected during the present study. Of particular interest is the sturgeon *Acipenser*. It is certainly not an ancestral type and some of its specializations are quite extreme, but in its external details it offers evidence of much value. This involves the three longitudinal series of body scutes, along the middorsal line, lateral lines from head to tail, and from each pectoral to pelvic fin. The first and last of these are in the situations of the hypothetical fin folds of the fin-fold theorists and are believed to be relics of extreme significance. In addition the anterior border of the pectoral fin appears to have been derived directly from one of these scutes.

Polypterus is of importance in being the less specialized of the only two crossopterygian genera now living, and it was undoubtedly from the rhipidistian crossopterygians of the Palaeozoic that the early amphibians arose (Baur, Watson, Broom, Gregory), for these are the only fishes known having vertebrae, skull and limb bones of a pattern that could have been ancestral. The fins of the living representative have, however, become specialized in a tangential direction.

There are almost as many ways in which the Teleosti may be arranged as there are

ichthyologists for the reason that the interrelationship of some of the groups is very obscure. Boulenger (1922) divides them into thirteen suborders as follows:

1. Malacopterygii, including tarpon, salmon, grayling, smelt, herring;
2. Ostariophysi, including characins, catfish, carp, loaches, tench;
3. Symbranchii, eel-shaped fish without paired fins;
4. Apodes, eels;
5. Haplomi, including cyprinodonts, pike;
6. Heteromi, mostly deep sea fish;
7. Catosteomi, sea horses, sticklebacks;
8. Percesoces, gars, mullets, barracuda, rudderfish;
9. Anacanthini, cod, haddock, pollock, and many deep sea forms;
10. Acanthopterygii, about 80 families of perch, blennies, cichlids, wrasses, mackerel, flatfish;
11. Opisthomi, eel-like, aberrant forms;
12. Pediculati, anglers;
13. Plectognathi, trigger and trunk fishes, mola.

Some of the teleosts are, of course, quite fantastically specialized and of no use to us, and even the simplest are far from generalized. The fins of some, however, exhibit a simple arrangement of their musculature, this varying largely with function, as discussed later. Features of the paired fins of teleosts appear to suggest that they have been derived from at least two, and possibly more, distinct sorts of very early acanthodians or other ancestral types, one of these having only paired fins in the pectoral region, and the other both pectoral and pelvic appendages, as considered more fully elsewhere.

GENESIS OF THE APPENDAGES

In examining the evidence pertinent to the derivation of the paired fins, a consideration of the two major theories so far advanced is essential. These are the Fin-fold Theory and the Gill-arch Theory.

Fin-fold Theory

The controversy over this hypothesis, advanced first by Balfour and by Thacher, has waged long and bitter. In its most logical form it postulates that the paired fins of fish represent opposite ends of a pair of continuous fins originally extending from the gills to the cloaca, and that median fins are similar remnants of a single fin in the middorsal line which extended around the tail to the cloaca, the arrangement having been much as now occurs in *Amphioxus*. It has been vigorously supported by a host of investigators, as already enumerated, and as energetically denied by others. Much impressive evidence may be marshalled to its support, as was done by Osburn (1907), but most of this is capable of being interpreted in other ways. On the whole the arguments should be more broadly interpreted, and the derivation from an actual longitudinal fin less uncompromisingly stressed.

The chief argument, perhaps, of the fin-fold protagonists is that the azygos and the paired fins of fish are similar in structure. This is only to be expected, for they are formed in the same manner from the same materials. The chief argument against this theory as usually advanced is the fact that although there is a suggestion of an epiblastic fold along the back in such elasmobranch types as *Scillium*, *Pristiurus*, and *Torpedo*, and even lateral ones from the cloaca to the pectoral region (Daniel, 1922), a continuous, longitudinal fin is not a character of a generalized vertebrate with fusiform body, but of the anguilliform, specialized type. Continuous fins have been developed by diverse sorts of fish, but only as an accompaniment of elongation of the body, as has been mentioned several times by Gregory (1915 and later). Finally it

appears that the evidence that the basic plan of the fin musculature was anteroposterior, instead of dorsoventral, renders the acceptance of the fin-fold theory in its usual form an impossibility, for such a fin must be operated by antagonistic dorso-ventral groups of muscles.

Gill-arch Theory

The alternative to the fin-fold theory has heretofore been the hypothesis that the pectoral fin at least is a derivative of the branchial apparatus, the girdle representing the branchial arch, and the skeleton of the fin proper a modification of the branchial rays. Originally advanced by Gegenbaur, this theory has attracted many supporters, some of whom have carried their arguments to fantastic lengths, claiming that the pelvic fins are also pharyngeal developments. As in numberless other cases the endeavor has usually appeared to be the proof of a favorite theory rather than the discovery of the truth.

As brought out in subsequent pages some of the facts used in support of the gill-arch theory are incontrovertibly persuasive, but all such facts can be interpreted in different ways. Some of the usual counter-arguments also are based upon misinterpretation of facts. Thus the statement by Dean (1902) that the pectoral girdle of *Cestracion* shifts forward during embryonic development was utilized by Osburn (1907) as disproof of the gill-arch theory. Actually this fact is merely an indication that the most posterior of the branchial arches, once present in an ancestor, have become atrophied in this form and the girdle takes a more advanced position as a result. An argument against the gill-arch theory is the claim that the pharyngeal structures develop in the medial or visceral part of the mesoderm and the shoulder girdle in the lateral or somatic part. But the incontrovertible proof that this theory cannot be fact is the circumstance that the intrinsic muscles of the paired fins are all innervated by somatic rather than visceral nerves.

Position of the appendages

There are undeniably critical areas for the elaboration of special details in all primitive animals. The midline dorsally, then around the tail and anteriorly as far as the cloaca, and the branchiocloacal lines are such, for it is only along these that fins developed. Furthermore there appears to be no limitation to the situation along these lines in which fins may occur. They may be in two pairs, at the opposite ends of the branchiocloacal line (elasmobranchs, dipnoans, ganoids, some teleosts); there may be only a pectoral pair (some ostracoderms, antiarchs), only a pelvic pair (arthrodires), or two pairs derived from consecutively contiguous somites (some acanthodians, and seemingly some teleosts). Living fish give the appearance of having been derived from the first and last of these categories, as already set forth (Howell, 1933c). Among teleosts at least the Malacopterygii conform to the same fin plan as elasmobranchs, dipnoans and ganoids, having true pelvic fins in addition to the pectoral pair, at opposite ends of the branchiocloacal line, the former basically for support and the latter for locomotion. But the teleostean suborders Anacanthini, Acanthopterygii, Pediculati and probably Plectognathi are largely composed of groups which appear to be derived from ancestors having no true pelvics. Instead the innervation suggests that in these a need for stabilizing appendages was supplied by the posterior elements of the pectoral series, which migrated ventrally to form so-called

ventral fins in neurologic sequence with the pectoral pair. It even appears possible for three pairs of appendageous structures to be derived from the original pectorals, as illustrated by the genus *Polynemus*(figs. 7, 8). This suggestion in regard to fin homology can be established or disproved only after much lengthy research.

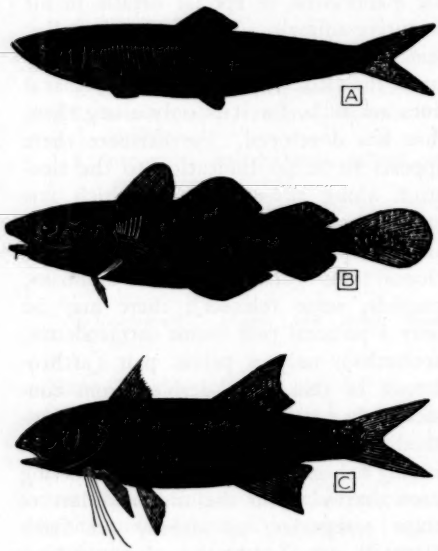

FIG. 7. (A) CLUPEA AND (B) GADUS, SHOWING DIAGRAMMATICALLY THE DISSIMILARITY IN THE ARRANGEMENT OF FIN NERVE DISTRIBUTION. (C) POLYNEMUS, WITH 3 ANTERIOR PAIRED FINS

The position of the fins can probably change within certain limits, and the position of a plurisegmental pelvic fin may, under particular conditions, simulate that of a ventral fin of few segments derived from a pectoral, but it is probable that such migration becomes severely restricted once the fin has become securely anchored to a girdle. The vertical position of the pectorals is also variable, these having assumed a position much higher upon the sides of some fish than of others.

Exoskeletal fin genesis

The belief is rather well established that the initiation of the fins was from dermal elements. As early as 1879 Mivart stated that paired limbs are essentially peripheral structures which have become more or less closely connected with the skeletal axis, while the limb girdles are

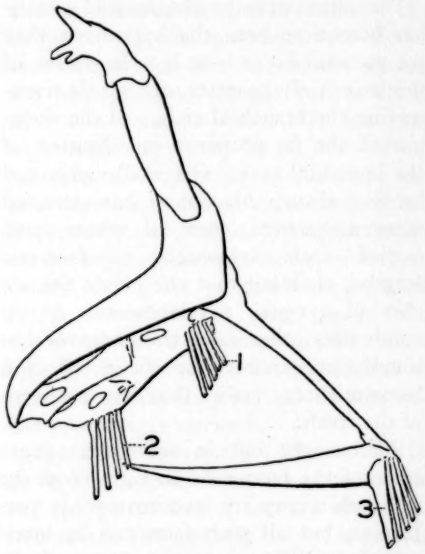

FIG. 8. LEFT SHOULDER GIRDLE OF POLYNEMUS, WITH 3 PAIRS OF ANTERIOR FINS: (1) TRUE PECTORAL, (2) PECTORAL FILAMENTS, (3) VENTRAL FIN

ingrowths from the bases of the limbs. Dermal fin rays are formed by fusion of lines of scales (in Actinopterygii) superseding the horny fin rays of an earlier period (Gregory, 1915); fin spines are clusters of metameric tubercles (Dean, 1907); and there are other similar statements in the literature.

Certainly fins could not have suddenly appeared as fins. There must have been a lengthy initial period during which they did not protrude sufficiently to be of use in locomotion, or in any other

definite action. It is likely that in the situations in which they later took form, along the midline and branchiocloacal lines, there were first series of longitudinal dermal structures of poor differentiation, and nothing is so likely as rows of scutes or enlarged scales, suggestive of those indicated in the apinnate anaspid *Birkenia*, and of the dermal structures that have now become hypertrophied in the sturgeon (fig. 9). Those scutes which were subjected to particular stresses during daily activities would naturally experience a stimulus for further differentiation, resulting in spines or rays that could have been used as props and as aids for wriggling over the bottom or for stirring up mud in search of food, and these are believed to have been the earliest definite

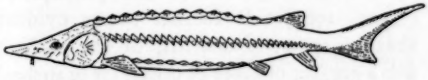

FIG. 9. THE STURGEON, ACIPENSER, SHOWING THE DISTRIBUTION OF LONGITUDINAL DERMAL STRUCTURES

functions of paired appendages. That the first critical functions were concerned with a habitat upon the bottom is indicated by the fact that the basically primitive types of all fish phyla show a heterocercal tail. Unpaired fins could have developed for equilibration at any time.

The appendages may have first taken the form of a heavy anterior ray and several successively smaller ones posteriorly, as suggested by a number of acanthodians such as *Parexus*, and by *Acipenser* (fig. 10). This may well have been the plan followed by those vertebrates with limbs having few somites. Or the initial plan may have involved the rather uniform development of a considerable number of dermal rods, suggested by elasmobranchs, with more numerous somites. It is evident that the original dermal rods, or dermotrichia, may break up into a number of more slender elements, so that the rays may be much more numerous than the somites contributing to the fin. In elasmobranchs there is but a single layer of these, but they are double in Teleostomi.

It seems extremely probable that at first each fin was as broad as the number of somites entering into its composition, with the dermal fin rays parallel. At this stage considerable migration of the fins was probably possible, by means of hypertrophy at one end accompanied by

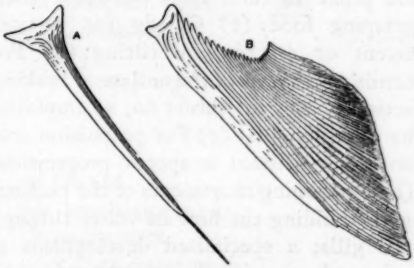

FIG. 10. RIGHT PECTORAL FIN OF THE STURGEON ACIPENSER, SHOWING HYPERTROPHIED DERMAL RAY UPON PREAXIAL BORDER: (A) ANTERIOR, AND (B) VENTRAL VIEWS

a compensating atrophy at the other. Later, however, there was concentration at the proximal bases of the dermotrichia, for increased mobility, brought about by differential growth of fin and body (Goodrich, 1930), and then concrescence or partial fusion at the base of the fins, not of the dermal rays but of basal cartilages. After this became at all pronounced any marked migration of the fins, at least to a greater extent probably than a very few segments, is considered to have been unlikely.

Stimulation by diverse uses

Before taking up specific anatomical evidence encountered in living fish, it

should be mentioned that after the paired fins became developed to the point where they were really of primary use to the animal they started to become further modified in a variety of directions, according to action. Such uses are of distinct sorts, as follows: (a) For propulsion over the bottom by appendages of the crutch-prop type: (b) As a horizontal rudder, much as an immobile dorsal fin is employed, a fairly primitive function, used, probably more or less exclusively by *Cladoselache*, and to a modified extent by recent sharks; doubtless correlated with the fact that sharks are prone to turn upon the back when grasping food: (c) Chiefly for vertical ascent or descent, by tilting: (d) For turning by means of the unilateral braking action of one out-thrust fin, as employed by most teleosts: (e) For propulsion oarwise, not utilized in speedy progression: (f) For fanning movements of the pectoral pair in aiding the flow of water through the gills; a specialized development of many teleosts: (g) For counteracting, by means of tilting of the fins, disturbance of equilibrium by water ejected through the gills; often an important function: (h) As simple props, to maintain an upright position when resting upon the bottom: and (i) for such functions as claspers, in correlation with reproductive processes. In addition fins are often highly modified for a variety of uses such as feelers, which tend to change them from a pinnate form. For (a) and (h) a spike-like fin would be most efficient; for (b) and (c), involving vertical steerage, a broad-based fin of the selachian or even the *Cladoselache* type; and for the remainder a fin with constricted base but with its plane tilted in various ways. This question of tilting has a pronounced effect upon the controlling musculature. Regardless of the position finally adopted preaxial and postaxial, dorsal and volar (if such a term be permissible in fish) is employed to denote the respective morphological aspects of the appendage.

ANATOMICAL EVIDENCE IN LIVING FISH

Pharyngeal evidence

Visceral details have had much influence upon the anterior limbs and must be considered. It may be accepted, I think, without going into particulars, that the entire oropharynx and branchial equipment innervated by the tenth nerve belongs with the viscera. It is also evident that the branchial segments pushed out between the lateral and ventral divisions of the somites, the original displacement of the latter perhaps having been helped by the development of the pronephros (Agar, 1908). It further seems evident that in some, if not all, of the earliest fish a greater number of posterior branchial arches was elaborated from vagus elements than is now found in their descendants, as indicated by the facts that in some elasmobranch embryos rudimentary gill arches occur posterior to the functional set (Daniel, 1922), and that in some forms there is a slight anterior migration of the pectoral limb during ontogeny (Dean, 1902). Nevertheless the pectoral appendages have been much displaced in a rearward direction, chiefly by the development of the gills, and they never regained their original position.

The cartilaginous gill arches have but slight interest for us in the present connection, but some of the pharyngeal muscles do have. In all fish one or more of the gill muscles, innervated by the vagus nerve, has posterior insertion upon the scapulocoracoid girdle in elasmobranchs, or upon its analogue, the clavicular girdle in other fish. Presumably in the tetrapod ancestor there were two

such muscles, one dorsally, representing the future m. trapezius, and the other ventrally, the precursor of the m. sternocleidomastoideus. In the dogfish the dorsal component alone is represented. It is in seeming series with the mm. interarcuales laterales, of the branchial series, farther forward. In bony fishes there are usually additional branchial slips attached to the girdle. In the cod

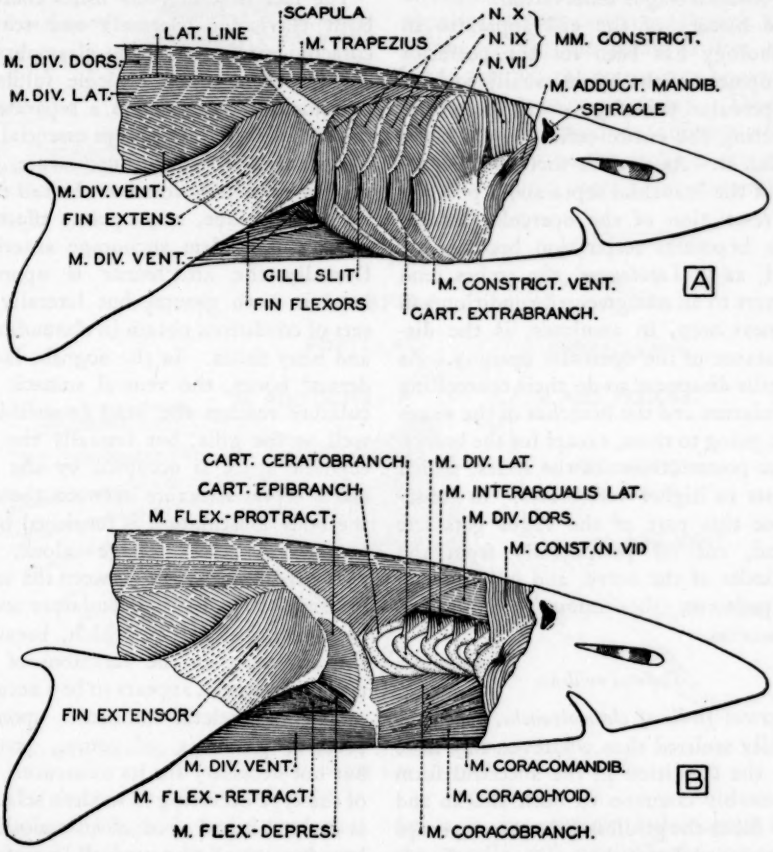

FIG. 11. MUSCULATURE OF THE DOGFISH (SQUALUS ACANTHIAS) IN THE REGION OF THE SHOULDER: (A) SUPERFICIAL ASPECT, AND (B) DEEPER VIEW OF BRANCHIAL DETAILS

It originates from the skin and fascia covering the suprascapular part of the dorsal division of trunk musculature (fig. 11), and extends ventrocaudally to insert upon both the epibranchial cartilage of the last gill arch and the anterior border of the ventral half of the scapular cartilage. (*Gadus*), for instance, two slips converge to the girdle from above and below, these being so situated as to suggest homologues of mm. trapezius and sternocleidomastoideus. In addition small branchial slips are at times attached to the dorsal part of the clavicular girdle. It is doubtful,

however, whether such slips can be homologized in different groups of fishes. The literature is confusing on this subject, for authors have frequently assigned the term trapezius to somatic muscle slips without vagus innervation.

The history of the gill apparatus in morphology has been for the posterior development of the hyoid usually to form an opercular covering, overlapping and protecting the entire series of gill clefts beneath it. As a result there was reduction of the branchial septa and a progressive restriction of the opercular orifice. When branchial respiration becomes reduced, as in *Lepidosiren*, the arches tend to revert to an unsegmented condition and the next step, in amniotes, is the disappearance of the opercular opening. As the gills disappear so do their controlling musculature and the branches of the vagus nerve going to them, except for the branch to the posteriormost of the series, which bersists in higher vertebrates. In consepuence this part of the vagus gets left behind, cut off peripherally from the remainder of the nerve, and is known in tetrapods as the ramus lateralis n. accessorius.

Skeletal evidence

Pectoral girdle of elasmobranchs. It must be fully realized that whatever may have been the condition in the ancestral form presumably common to both sharks and bony fishes the girdles of these two groups have been elaborated on plans so different that they can hardly be compared, detail by detail, although the skeletal features, as a whole, have the same functions in both. It seems likely that the common ancestor of the two groups had exoskeletal appendages, but it is not improbable that it had not as yet established endoskeletal anchorage for the controlling musculature.

There are at least four possible factors that have been influential in the development of the anterior girdles: (a) somatic, concerning the trunk proper, (b) exoskeletal, (c) branchial, and (d) the possible effect of the intestinal viscera.

The fact that in bony fishes there are both clavicular (dermal) and scapulocoracoid girdles, while in elasmobranchs a single cartilaginous girdle fulfils the functions of both, makes a separate discussion of these two groups essential.

In order that trunk musculature, operated in swimming to move the tail in the horizontal plane, may operate effectively it must have firm anchorage anteriorly. Dorsally the attachment is upon the head in both groups, but laterally two sets of conditions obtain in elasmobranchs and bony fishes. In the dogfish, lacking dermal bones, the ventral somatic musculature reaches the head (mandible) as well as the gills, but laterally the postcephalic space is occupied by the gills, and a septal structure between these and the body musculature is furnished by the scapulocoracoid cartilage alone. This also provides a septum between the ventral division of the body musculature and the hypobranchial group, which, because of the difference in the functions of these two components, appears to be a necessity.

The exoskeletal influence upon the pectoral girdle is, of course, profound but not necessary for its existence. A fin of the type occurring in modern selachians is in mechanical need of an endoskeletal base for articulation, as well as to furnish origin to its musculature. *Cladoselache* must have had such a fin base anchorage, else the cartilaginous radialia could not have reached the degree of development which they did.

An additional stimulus operating upon the pectoral girdle of elasmobranchs is that of posterior anchorage for the branchial apparatus, and as a strut be-

tween the dorsal and somatic divisions of the trunk, in order that the gills may not be squeezed between them. In this

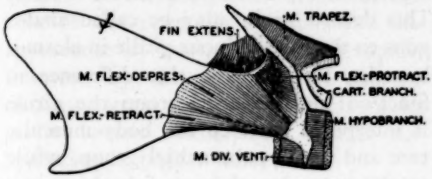

FIG. 12. MUSCULATURE OF THE VENTRAL SURFACE OF THE PECTORAL FIN, WITH PREAXIAL FIN BORDER ELEVATED, OF SQUALUS ACANTHIAS

means of the septum transversum, dividing the pericardium from the metacoele.

In the dogfish (as in *Heterodontus*) the girdle consists of a U-shaped cartilage continuous in the midventral region, but in *Heptanchus* it is there separated by an unpaired sternal cartilage (Daniel, 1922). In the sharks the girdle is free above but in the rays the points may be attached to each other or to a vertebra. The angle of slope varies much in different groups. In elasmobranchs the girdle is designated scapulocoracoid merely for convenience,

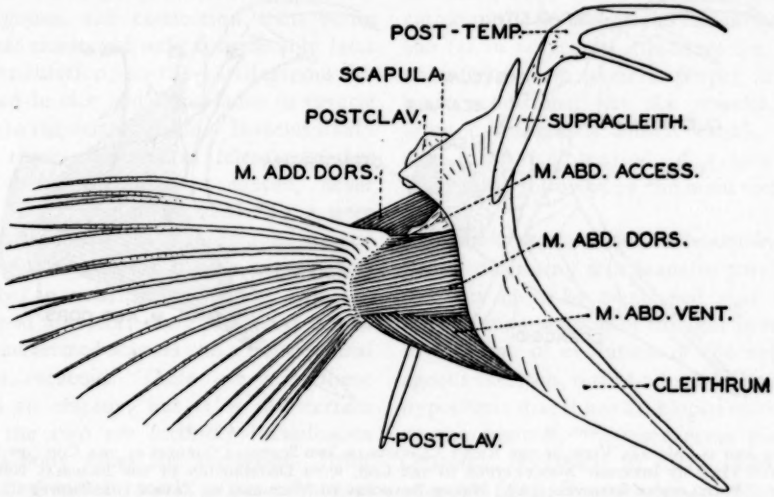

FIG. 13. LATERAL VIEW OF THE RIGHT CLAVICULAR GIRDLE, PECTORAL FIN, AND ITS INTRINSIC MUSCULATURE IN THE COD (GADUS)

group too, although it is believed that the pectoral girdle would be present even were there no paired fins, the former has undoubtedly been much modified and strengthened by the action of these appendages, in furnishing attachment for the intrinsic muscles. The fourth stimulus, of unknown strength, that has operated upon the selachian girdle is correlated with the fact that it affords attachment for the anterior viscera, by for it is not entirely homologous with the scapula and coracoid of bony vertebrates. In the dogfish the only movable joint to the girdle is at the juncture of the dorsal with the lateral group of trunk musculature, where a small suprascapular cartilage articulates with the dorsal end of the scapula (fig. 13). The part of the selachian girdle just below the fin joint is pierced by the coracoid foramen (sometimes by a second) through which pass

the diazonal nerves supplying the original protractor musculature of the fin.

The pectoral girdle in bony fishes. In the bony fishes, as in the piscine ancestor of tetrapods, the very different basic conditions involved an extensive array of dermal bones, mechanically perfected probably before the appendages had had endoskeletal effect. Hence it is believed that this system, rather than the cartilaginous components as popularly stated, really constituted the primary girdle. Elements of this dermal system finally in teleosts the dermal elements typically present are post-temporal above, supracleithrum, and cleithrum below, although supernumerary bones occur in some sorts. This dermal girdle may be called analogous to the cartilaginous girdle in elasmobranchs, but there is this difference in function: in the latter group the girdle is interposed between the body musculature and the hypobranchial group, while in the majority of bony fish there is a postclavicle (fig. 14) so-called, generically variable in development, which in such a

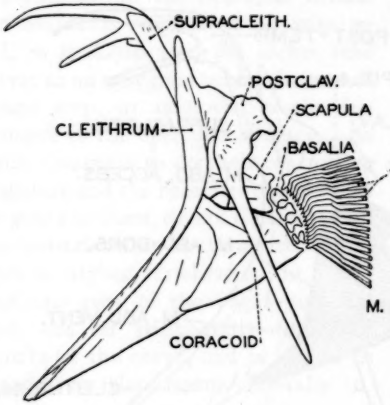

FIG. 14

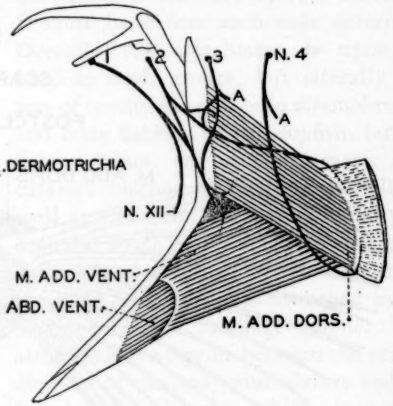

FIG. 15

FIGS. 14 AND 15. MEDIAL VIEW OF THE RIGHT CLAVICULAR AND SCAPULAR GIRDLES OF THE COD (ON LEFT). MEDIAL VIEW OF INTRINSIC MUSCULATURE IN THE COD, WITH DISTRIBUTION OF THE BRACHIAL NERVES; POSTCLAVICLE REMOVED; (AA) NERVE BRANCHES TO MYOMERES OF TRUNK (ON RIGHT)

came to encircle the gill openings, both for protecting the gills with the help of the operculum, for furnishing support for the branchial structures, and to provide necessary anterior anchorage for the body musculature.

This so-called clavicular girdle in the bony fishes is composed of elements that vary considerably in the major groups. Both clavicle and cleithrum occur in Crossopterygii, Chondrostei, and Dipnoi, but in Holostei and Teleostei the clavicle has been lost (Gegenbaur, 1895), so that form as the cod more nearly resembles a first rib in that it has developed in a myoseptum between the trunk muscles proper and the hypobranchial musculature, the latter having anterior attachment to the cleithrum, or clavicle when present. Above, the much reduced lateral trunk division is attached to a dorsocaudal process of the postclavicle. In bony fishes the clavicular girdle first provides attachment for the posteriormost of the branchial series, the homologues of the mm. trapezius and sternocleidomastoideus

in the tetrapod ancestor at least, and these latter appear to have shifted, at a later date, to the developing cartilaginous girdle. In the postpiscine stage the closure of the opercular opening and disappearance of internal gills was rapidly followed by the reduction of the encircling dermal shield and the clavicular girdle became incomplete, almost disappearing in higher tetrapods.

In this group it is considered that the cartilaginous elements of the scapular girdle had little or nothing to do with the clavicular girdle at first, being merely contiguous, the connection then being by soft tissue and only considerably later by articulation, as the cartilaginous increased in size and importance in inverse ratio to the dermal girdle. It seems likely that these elements in teleosts, rather than being secondarily reduced, never were larger than at present. They were initiated in intermuscular septa and marked points of divergent muscle stress. Primarily, in existing bony fishes as in the tetrapod ancestor, there is a more dorsal element termed scapula and a more ventral called coracoid. These are convenient terms to employ, but it is not certain that the two are precisely homologous in all bony fishes and tetrapods. After all, they merely mark points of antagonistic muscle stresses and may or may not be equal to the same thing in all cases. Some groups of Teleostei (Malacopterygii, Ostariophysi) have an additional element of the shoulder known as the mesocoracoid. Neither should an attempt be made to homologize this element with any structure in tetrapods, nor even, perhaps, with the so-called mesocoracoid arch of Holostei and Chondrostei, although the homologue of the latter does seem to occur in some of the lower tetrapods.

Foramina in the scapula girdle of ganoids, or Actinopterygii, consist of the coracoid, glenoid, and supraglenoid foramen, as discussed by Romer (1924). The first of these is for the transmission of the diazonal nerves and is of great morphologic value in vertebrates, but it is doubtful whether the other two are of broad phylogenetic significance. The homologue of the coracoid foramen in teleosts is the fenestration between the scapula and coracoid.

Consideration of the anatomical details of existing dipnoans and ganoids, even including *Polypterus*, shows that specialization of the fin and girdles has progressed too far in tangential directions for us to gain from them alone a proper idea of basic conditions, but the muscles, and often cartilaginous muscle canals, indicate much modification of a sort that was hardly followed by the main tetrapod line.

Appendageous skeleton in elasmobranchs. Before discussing selachians in particular the fact must be mentioned that there are two main schools of thought in regard to the line of evolution of the appendageous skeleton, one of which follows the hypothesis that it has developed according to the biserial, archipterygium plan of *Ceratodus*, occurring in early Dipnoans, crossopts, and *Pleuracanthus*, as advanced by Gegenbaur and followed by Gunther, Braus, Huxley, Howes and others, or according to the pleurorarchic plan, with basal axis, and radials along the outer edge, as Wiedersheim, Regan, Woodward, Sewertzoff and others have believed. Either thesis can be argued with plausibility, according to the ideas suggested in figure 16. It is rather likely that there developed a bar-like series of cartilages at the base of the primitive, unconcentrated fin (fig. 16, B) which could evolve in both directions. From a fairly generalized stage (fig. 16, D) could have come

possibly *Polypterus* (although its resemblances are probably of a convergent nature) and probably the arrangement most typical of selachians, involving three basalia comprising propterygium anteriorly, mesopterygium, and metapterygium posteriorly, articulating with the girdle. The embryonic condition bears out this sequence, for there is at first a single cartilaginous bar representing the metapterygium from which extend radialia; the bar seems later to become the main axis secondary to which arises the meso-, and finally the propterygium (Daniel, 1922), the smallest and apparently the most recent of the three elements. Gegenbaur and Woodward also considered the metapterygium as the main axis, although Huxley, Balfour, and Howes especially, have maintained that this rôle is filled by the mesopterygium. Goodrich considers that such precise commitments are unwise, and as a matter of fact there may never have been strict uniformity among the different groups. Thus in *Heterodontus* the propterygium appears at times to be fused with the mesopterygium, and occasionally, in a species of *Scymnus*, there is only a single basalium (Daniel, 1922).

The possibility must be entertained that the structure at the base of the pectoral fin in the remains of *Cladoselache* was nephritic rather than cartilaginous. At any rate, however, it must have had basal cartilages, and the discrete nature of the fin base suggests that these may have had a longitudinal form. The fact that the dermotrichia, if actually present, were relegated to the posterior border of the fin in cladoselachians, and the great development of the radialia indicate not only that the musculature was well developed, but also that the entire fin

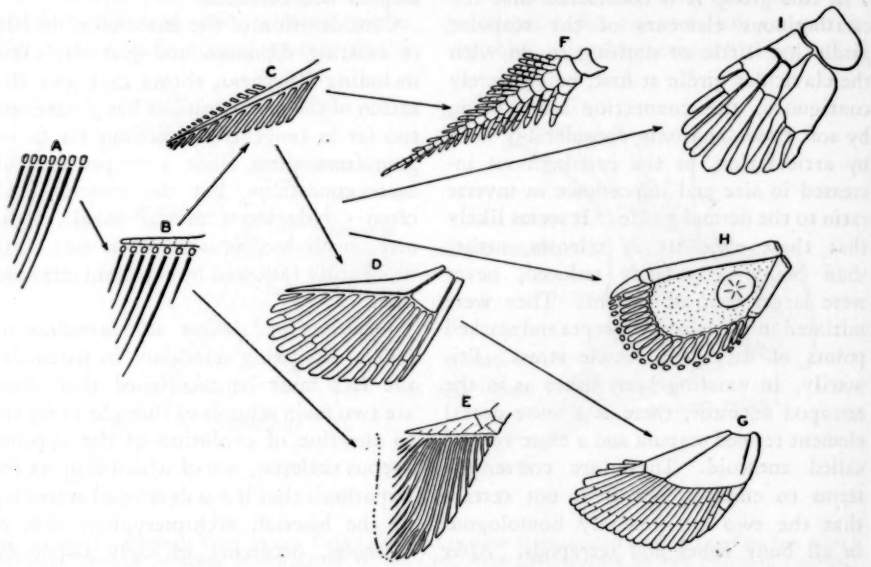

FIG. 16. HYPOTHETICAL MORPHOGENESIS OF THE PECTORAL LIMB IN FISH: A, B, C, D, HYPOTHETICAL STAGES; E, CLADOSELACHE; F, CERATODUS; G, SQUALUS; H, POLYPTERUS; I, SAURIPTERUS. PREAXIAL BORDER OF THE FIN TOWARD THE RIGHT

equipment exhibited a definitely specialized condition in all features except the unconcentrated bases of the radials, instead of a basically primitive one as usually claimed.

Typically the selachian propterygium distally bears but one (occasionally two) large, proximal radialium while the other two bear many. This row of radialia is distally followed by two more rows, the most distal of which appears usually, if not invariably, to consist of a number twice as great as that of the nerves supplying the fin. The radials arise not as outgrowths of the girdle but as differentiations of the mesenchyme in situ (Balfour, Ruge, Swinnerton, Derjugin).

In selachians the joint with the fin base is a simple articulation enclosed by a virtually continuous, fibrous capsule permitting more movement in the axial than the vertical direction, but in most bony fishes there is no true skeletal joint at this point, the elements not being sufficiently approximated.

As already stated the single layer of dermotrichia in selachians has been derived from a variably considerable number of body segments, and it is personally considered likely, although by no means certain, that the anteriormost was never much heavier than the others in this group. In fact it seems likely that the dermal element that was originally anteriormost in this group has disappeared, as explained in connection with the musculature.

Appendageous skeleton in bony fishes. The earliest types of bony fishes had a fin essentially of the biserial pattern, but hardly in its extreme form as now encountered in *Ceratodus*. This type of fin is suited to a rather sluggish life on the bottom, not to a predaceous, active, free swimming existence, which tends to develop a uniserial fin. Among fossil fishes the only group that fulfills the anatomical requirements necessary in the tetrapod ancestor is the rhipidistian crossopterygians, with what may be called a generalized biserial fin. Thus the fin of *Sauripterus* (fig. 16, I) and to a lesser extent of *Eusthenopteron*, provides us with a very satisfactory plan for the elaboration of the tetrapod limb. A discussion of the significance of this pattern belongs more strictly in the chapter on amphibians than here, however. The pectoral appendage of living crossopts may be considered as uniserial now, but it is believed to have become secondarily so, through shortening and loss of a humeral segment.

The most useful fin for a fish of active, free-swimming habits is one with an extremely short base, and a uniserial appendage of this pattern is the one encountered in all living bony fishes except dipnoans. Although the basal cartilages may be of some considerable length, especially posteriorly (as in *Acipenser*), they are located within the body contour (with *Polypterus* and a few aberrant sorts as partial exceptions) and more frequently take the form of a single row of insignificant nodules between the girdle and dermal fin. So this feature of the teleost fin base is believed to have degenerated from an ancestral condition involving moderate development in the biserial direction.

Swinnerton (1906) found that in the teleost *Gasterosteus* there is an embryological tendency for the glenoid line (fin angle) to rotate from a nearly horizontal to a vertical position. This tilting occurs in response to a variety of functional stimuli, as already mentioned, and the direction is typically one that involves elevation of the preaxial and depression of the postaxial border. As a result the "volar" aspect of the fin, in sorts in which this tilting has occurred, is di-

rected laterally and the dorsal surface medially.

The course of development probably followed in bony fishes by the dermotrichia has already been outlined, and mention made of the probability that the plan involved the original hypertrophy of one of the anterior dermal spines, which were fewer in number than in selachians. A circumstance needing interpretation is the fact that in bony fishes the dermotrichia occur in two layers. In *Polypterus*, say, it is possible that this could have been achieved by alternate staggering of the elements of an originally single layer, but this possibility can not be entertained in the case of teleosts, in at least many of which nerves pass between the two layers from each fin border. To explain this it seems necessary to postulate that either the dermotrichia are derived from two parallel rows of dermal scutes, which is not likely, or else that the scutes of the single row, in the ancestral condition, had bifurcated bases, which later became accentuated.

Neurological evidence

Most of the evidence based on the nervous system has already been discussed and repetition here would be useless. There are a few additional details to be considered, however.

It is clear that the fin musculature was derived from a number of body segments that theoretically was precisely the same as the number of spinal nerves entering the extremity, although in the course of phylogeny it is not inconceivable that one or two of these might be relinquished as the need arose. In practically all living vertebrates, however, there has been a concentration of the fin base, to increase mobility and effectiveness, and after this concentration became pronounced it is believed that the number of nerves supplying the appendage was fixed, at least within very narrow variational limits, for all time.

Constriction of the fin base started posteriorly and progressed forward. As a result the nerves entering the fin are gathered together at the fin base, the posterior elements of the series having a forward inclination to this point. But the entire fin has been displaced in a caudal direction by the development anterior to the girdle of the branchial apparatus, and so the anterior brachial nerves are also inclined, but to the rear.

It is believed that the variation in the number of brachial nerves in fish, especially elasmobranchs, is not a late development but reflects the fact that the basic ancestors of these diverse types elaborated their appendages out of a variable number of body segments, and that the only late change in the number of nerves entering the limb might be brought about by the constriction or expansion, within very narrow limits, of the corresponding motor nuclei in the cord.

In elasmobranchs a variable number of spinal nerves supply the fin and these are always more numerous than in bony fishes. In the dogfish (*Squalus*) they usually number ten, and are arranged in beautifully simplified manner, practically free from anastomoses (fig. 17). Typically the three anteriormost nerves pass through the coracoid foramen to the lateral surface of the fin and supply the protractor musculature—the anterior part of the flexor group. Posterior to these diazonal nerves the remainder of the brachial series supply all the extensor and the rest of the flexor musculature. Each of the brachial nerves except those of the diazonal group contributes a small branch to the corresponding trunk segment.

In living fish other than elasmobranchs the typical number of spinal nerves supplying the pectoral limb appears to be four or five, but the exact nervous pattern varies according to group to such a degree that it is impossible to pick any one as basic. Even in *Polypterus* the secondary specialization has likely been sufficient to obscure the picture probably typical of the generalized crossopterygians. Neither is electrical stimulation of the nerves of definite help, for the results are too diffuse in character to indicate the precise segmental origin of the muscle divisions.

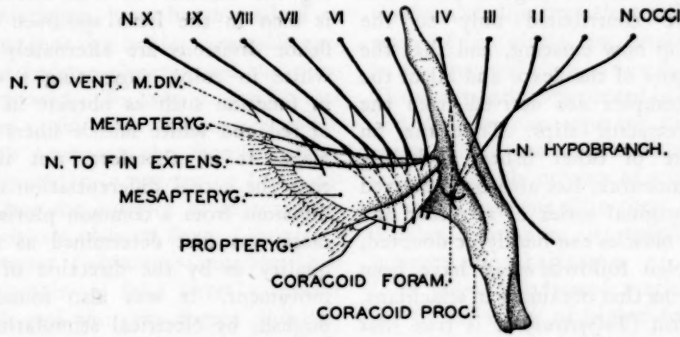

FIG. 17. DISTRIBUTION OF THE BRACHIAL NERVES OF THE DOGFISH SQUALUS IN RELATION TO THE GIRDLE AND APPENDAGE OF THE RIGHT SIDE

In some fish (as *Polypterus*) the first brachial nerve appears to supply only the flexor (protractor) musculature of the fin, while in others it innervates both extensor and flexor components. The diazonal nerve branches, passing through a fenestration between scapula and coracoid bones, appear to be derived from the first nerve only in some fish (as *Amia*), second only (as *Polypterus*), first two (as *Cyprinus*), or first three (probably most fish, as in *Gadus*).

The brachial nerves of fish may be grouped into those that pierce the coracoid foramen, the branches that supply the other flexors, and those belonging to the remainder of the extensors. I regard it as impossible, however, to homologize these with the suprascapular, extensor, and flexor nerves of the tetrapod limb (Romer, 1924), for the respective muscle divisions supplied by these nerves vary too much even within the single class Pisces.

Myological evidence

In several selachians that have been investigated it has been found (Dohrn; Braus, 1899; Goodrich, 1906) that each trunk myomere gives rise to a pair of muscle buds along the line of the paired fins. Those buds destined to take part in the fins develop and the remainder disappear. The latter may be interpreted as vestiges representing muscle slips which originally inserted upon a continuous series of dermal structures along the branchiocloacal line. It seems certain that the initiation of the appendageous musculature was in the form of a slip from each involved body segment to the corresponding dermal element, and that later these aligned themselves into a muscular complex for retraction and another for protraction. The latter group

could have been derived in a manner suggested in figure 4 of Part I, by secondary atrophy of the anteriormost dermal structures and attachment of their muscle slips to a more posterior ray, or else protractor slips might have differentiated entirely independently. At any rate it seems clear that longitudinal fission into a dorsal or extensor group and a ventral or flexor group came only later, as there was experienced need for the operation of the fin in these two directions.

The nerve distribution in the dogfish shows that in this selachian, as doubtless in others, all of the original protractor musculature contributed only to the flexor group now existing, and that the posterior part of the flexor and all of the extensor complex are derived from the original retractor slips. That the fin musculature of other fishes, including tetrapod ancestors, has also been derived from an original series of retractor and protractor muscles can hardly be doubted, but the plan followed may have been different from that obtaining in selachians. In some fish (*Polypterus*) it is true that the first brachial element appears to have contributed to the flexor musculature alone, but in most sorts both flexors and extensors are supplied by the first as well as subsequent brachial nerves. Unfortunately the picture in bony fishes, although at first glance simple, has passed through too many phases to be interpreted with certainty. It can merely be said that the longitudinal splitting of the retractor-protractor series into extensor-flexor groups may well have been determined on a more uniform basis than in the selachians by the fact that in bony fishes the dermotrichia occur in two layers, with nerve between, suggesting that the original dermal elements may have had a tendency toward bifurcation at the base, this feature largely determining the later division of the musculature.

In the bony fishes there occur, in different sorts, several slips with vagus innervation inserting upon the clavicular girdle, and it seems unwise to attempt to homologize any of these with trapezius and sternocleidomastoid of tetrapods.

In the dogfish the alignment of the intrinsic pectoral fin musculature is into a single extensor component, and three, or even four, flexor divisions, all of which are arranged to good advantage for moving the member in four directions. It is seen in the fresh specimen that the flexor divisions are alternately red and white in color, suggesting a difference in function such as obtains in the case of red and white muscle fibers of mammals. It is, therefore, not impossible that the actual differentiation of muscle divisions from a common plurisegmental mass was first determined as much by quality as by the direction of required movement. It was also found in the dogfish, by electrical stimulation of the brachial nerves, that each of these supplies a consecutively smaller muscle area progressing posteriorly, so that the area affected through the ninth or tenth nerve is but a couple of millimeters in width (Howell, 1933a).

In *Ceratodus* the fin musculature is entirely too complex to be indicative of a basic pattern, in *Protopterus* the intrinsic system is too degenerate, and in the other bony fishes it has probably been secondarily simplified to confusing degrees. One of the chief difficulties has been introduced by the tilting of the fin experienced by most bony fishes. In a teleost with simple fin action such as the cod (*Gadus*), the typical scheme of muscle arrangement involves a superficial and a

deep flexor (abductor), the two converging at an angle, and similar extensor (adductor) divisions, in addition to one or two small, accessory muscles. These presumably act to expand and fold the fin, as well as to abduct and adduct it. It is as simple an arrangement as could be really effective, but has evidently been evolved from a more elaborate pattern. Instead of a fin with elongate base, such as in *Ceratodus*, a free-swimming, active type of fish demands paired fins of extremely short base, and the modern type of teleost fin has been the result.

In response to functional requirements of one sort or another the pectoral fins in many teleosts have become tilted or rotated so that the border originally preaxial has become elevated and the postaxial depressed. To keep pace with this alteration in fin plane and to accomplish the work necessary the muscle origins have migrated to a greater or lesser degree. Thus the anterior or more superficial divisions of both flexor (abductor) and extensor (adductor) muscles have moved dorsalward (the latter a greater distance), and the two deeper divisions of both groups somewhat ventralward, instead of the extensors being above and the flexors below the fin. All four muscles are really more intimately concerned at origin with the cleithrum than with the cartilaginous girdle, but in addition the scapula now furnishes attachment to one extensor and one flexor, and the coracoid to the other extensor and second flexor.

The latter circumstance introduces a serious problem into the history of the shoulder girdle. It hinges on the question of whether the piscine forms ancestral to tetrapods had pectoral fins already tilted to the vertical position, or whether the originally horizontal posture of these members persisted throughout the aquatic period. If the former were the case then some of our accepted concepts of bone-muscle relationship in the shoulder would need revision. The point can only be decided after a study of conditions in postpiscine stages.

In *Polypterus* a third muscle element—a dilator, so-called—occurs in both abductor and adductor groups, as is also the case in many teleosts, but in the former genus the basal elements of the fin have degenerated and the muscular condition can not be considered as basic. On the whole the arrangement is not essentially different from that typical of teleosts.

Extrinsic muscles of the shoulder, in the form of slips from the trunk to various parts of the girdle, are better developed in the sturgeon than in any fish dissected. They are poorly represented in all, though, and lacking, as separate divisions, in most. They can appear in response to such a variable number of stimuli and in so many patterns that their plan in individual instances is totally without interpretable significance.

As already indicated much that is of use in the study of higher forms can be gained from the details of the skeleton in fish, and much from the nerves as well. From the muscles, however, not so many dependable facts can be gleaned, for it is doubtful that the plan now encountered in any living fish reflects conditions in the immediate piscine ancestor of tetrapods. One can with ease divide the muscles of the pectoral fin of all groups of fishes into prime movers and their antagonists, or the usual flexor-extensor scheme, as has been done in the past, but the derivation of these elements, segmentally considered, is so diverse in different fishes, that such division on a functional basis can have no homological meaning.

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LIST OF LITERATURE

AGAR, W. E. 1908. The development of the anterior mesoderm, and paired fins with their nerves, in *Lepidosiren* and *Protopterus*. *Trans. Roy. Soc. Edinburgh*, vol. 45, pp. 611–639.

ALLEN, W. F. 1917. Distribution of the spinal nerves in *Polistotrema* and some special studies on the development of spinal nerves. *Jour. Comp. Neurol.*, vol. 28, pp. 137–213.

BALFOUR, F. M. 1881. On the development of the skeleton of the paired fins of Elasmobranchii, considered in relation to its bearings on the nature of the limbs of the vertebrates. *Proc. Zool. Soc. London*, pp. 656–671.

BAUR, G. 1885. Ueber das Archipterygium und die Entwickelung des Cheiropterygium aus dem Ichthyopterygium. *Zool. Anz.*, Bd. 8, pp. 663–666.

BOLK, L. 1899. Die Segmentaldifferenzirung des menschlichen Rumpfes und seiner Extremitäten. *Morph. Jahrb.*, Bd. 27, pp. 630–711.

BRAUS, H. 1898. Ueber die Innervation der paarigen Extremitäten bei Selachiern, Holocephalen und Dipnoern. *Jenaische Zeitschr. Naturwiss.*, Bd. 31, pp. 239–467.

———. 1899. Beiträge zur Entwicklung der Muskulatur und des peripheren Nervensystems der Selachier. *Morph. Jahrb.*, Bd. 27, pp. 415–496, 501–629.

———. 1900. Die Muskeln und Nerven der Ceratodusflusse. *Jenaische Denkschr.*, Bd. 4, pp. 209–217.

BREDER, C. M. JR., 1926. The locomotion of fishes. *Zoologica*, vol. 4, no. 5, pp. 159–297.

BRIDGE, T. W., and G. A. BOULENGER. 1922. Fishes, Ascidians, etc. Cambridge Nat. Hist., *London*, 760 pp.

BROOM, R. 1913. On the origin of the cheiropterygium. *Bull. Amer. Mus. Nat. Hist.*, vol. 32, pp. 459–464.

CILIMBARIS, P. A. 1910. Histologische Untersuchungen über die Muskelspindeln der Augenmuskeln. *Arch. mikr. Anat.*, Bd. 75, p. 692.

CIPOLLONE, L. T. 1897. Ricerche sull'anatomia normale e patologica delle terminazione nervose nei muscoli striati. *Suppl. Annuali di Medicina Navale*, vol. 3, p. 282.

COPE, E. 1890. The homologies of the fins of fishes. *Amer. Nat.*, vol. 24, pp. 401–423.

DANIEL, F. 1922. The Elasmobranch Fishes. Univ. Calif., 334 pp.

DEAN, B. 1894. Contribution to the morphology of *Cladoselache* (*Cladodus*). *Jour. Morph.*, vol. 9, pp. 87–114.

———. 1896. The fin-fold origin of the paired limbs, in the light of the Ptychopterygia of Palaeozoic sharks. *Anat. Anz.*, Bd. 11, pp. 673–679.

———. 1907. Notes on acanthodian sharks. *Amer. Jour. Anat.*, vol. 7, pp. 209–226.

DERJUGIN, K. 1910. Der Bau und die Entwicklung des Schultergürtels und der Brustflossen bei den Teleostiern. *Zeitschr. wiss. Zool.*, Bd. 96, pp. 572–653.

DOHRN, A. 1884. Die paarigen und unpaaren Flossen der Selachier. *Mittheil. Zool. Station Neapel*, Bd. 5, p. 161–195.

GEGENBAUR, C. 1865. Untersuchungen zur vergleichenden Anatomie der Wirbeltiere. Heft II. Brustflosse der Fische. *Leipzig*.

———. 1872. Ueber das Archipterygium. *Jenaische Zeitschr. Med. Naturwiss.*, Bd. 7, pp. 131–141.

———. 1876. Zur Morphologie der Gliedmassen der Wirbelthiere. *Morph. Jahrb.*, Bd. 11, pp. 396–420.

———. 1895. Das Flossenskelet der Crossopterygier und das Archipterygium der Fische. *Morph. Jahrb.*, Bd. 22, pp. 119–160.

———. 1898. Vergleichende Anatomie der Wirbelthiere. *Leipzig*.

GOODRICH, E. S. 1906. Notes on the development, structure, and origin of the median and paired fins of fish. *Quart. Jour. Micr. Sci.*, vol. 50, pt. 2, pp. 333–376.

———. 1930. Studies on the Structure and Development of Vertebrates. *London*, 837 pp.

GREGORY, W. K. 1912. Notes on the origin of the paired limbs of terrestrial vertebrates. *Ann. N. Y. Acad. Sci.*, vol. 21, pp. 219–220.

———. 1915. Present status of the problem of the origin of the Tetrapoda with special reference to the skull and paired limbs. *Ann. N. Y. Acad. Sci.*, vol. 26, pp. 317–383.

———. 1933. The new anthropogeny: twenty-five stages of vertebrate evolution, from Silurian chordate to man. *Science*, vol. 77, pp. 29–40.

HALLER, B. 1905. Über den Schultergürtel der Teleostier. *Arch. Mikr. Anat.*, Bd. 67, pp. 231–266.

HAMMERSTEN, O. D. 1911. Über die Innervation der Bauchflossen bei den Teleostiern. *Morph. Jahrb.*, Bd. 42, pp. 665–697.

HARRISON, R. G. 1894. The development of the fins of teleosts. *Johns Hopkins Univ. Circ.*, vol. 13, no. 111, pp. 59–61.

———. 1895. Die Entwickelung der unpaaren und paarigen Flossen der Teleostier. *Arch. mikr. Anat.*, Bd. 46, pp. 500–578.

HERRICK, C. J. 1899. The cranial and first spinal nerves of *Menidia;* a contribution upon the nerve components of the bony fishes. *Jour. Comp. Neurol.*, vol. 9, pp. 154–455.

HOWELL, A. B. 1933a. The architecture of the pectoral appendage of the dogfish. *Jour. Morph.* vol. 54, pp. 399–413.

———. 1933b. The architecture of the pectoral appendage of the cod fish. *Anat. Rec.*, vol. 56, pp. 151–158.

———. 1933c. Homology of the paired fins in fishes. *Jour. Morph.*, vol. 54, pp. 451–457.

HUMPHRY, G. M. 1872a. The muscles of *Ceratodus*. *Jour. Anat. Physiol.*, vol. 6, pp. 279–287.

———. 1872b. Observations in Myology, Including the Myology of Cryptobranch, *Lepidosiren*, Dog-fish, *Ceratodus* and *Pseudopus pallasii*, with the Nerves of Cryptobranch and *Lepidosiren* and the Disposition of Muscles in Vertebrate Animals. *London*, 192 pp.

IHLE, J. E. W., D. P. VAN KAMPEN, H. F. NIERSTRAZ, and J. VERSLUYS. 1924. Leerboek der Vergelijkende Ontleedkunde van de Vertebraten. *Utrecht*, Bd. 2, 504 pp.

JAEKEL, O. 1909. Ueber die Beurteilung der paarigen Extremitäten. *Sitz. Ber. Kön. Preuss. Akad. Wiss.*, pp. 707–724.

KAPPERS, C. U. A. 1911. Weitere Mitteilungen über Neurobiotaxis. VI. The migrations of the motor cells of the vagus group and the phylogenetic differentiation of the hypoglossus nucleus from the spino-occipital system. *Psychiat. en Neurolog. Bl.*, Bd. 15, pp. 408–427.

KLAATSCH, H. 1896. Die Brustflosse der Crossopterygier. Ein Beitrag zur Anwendung der Archipterygiumtheorie auf die Gliedmassen der Landwirbelthiere. Festsch. z. 70. Geburtstage v. C. Gegenbaur, Bd. 1, p. 259–392.

KRYZANOVSKY, S. 1927. Die Entwicklung der paarigen Flossen bei *Acipenser*, *Amia* und *Lepidosteus*. *Acta Zool.*, Bd. 8, pp. 277–352.

MAURER, F. 1892. Der Aufbau und die Entwicklung der ventralen Rumpfmuskulatur bei den urodelen Amphibien und deren Beziehung zu den gleichen Muskeln der Selachier und Teleostier. *Morph. Jahrb.*, Bd. 18, pp. 76–179.

MIVART, ST. G. 1879. Notes on the fins of elasmobranchs, with considerations on the nature and homologues of vertebrate limbs. *Trans. Zool. Soc. London*, vol. 10, pp. 439–484.

MOLLIER, S. 1893. Die paarigen Extremitäten der Wirbeltiere. I. Das Ichthyopterygium. *Anat. Hefte*, Bd. 3, pp. 1–160.

MÜLLER, E. 1909. Die Brustflosse der Selachier. *Anat. Hefte*, Bd. 39, pp. 469–601.

NISHI, S. 1922. Zur Morphologie des M. trapezius. *Folia Anat. Japon.*, Bd. 1, pp. 175–181.

NORRIS, H. W., and S. P. HUGHES. 1920. The cranial, occipital, and anterior spinal nerves of the dogfish, *Squalus acanthias*. *Jour. Comp. Neurol.*, vol. 31, pp. 293–395.

OSBURN, R. C. 1906. The origin of vertebrate limbs. Recent evidence upon this problem from studies on primitive sharks. *Ann. N. Y. Acad. Sci.*, vol. 17, pp. 1–21.

———. 1907. Observations on the origin of the paired limbs of vertebrates. *Amer. Jour. Anat.*, vol. 7, pp. 171–194.

PARKER, W. K. 1868. A Monograph on the Structure and Development of the Shoulder-girdle and Sternum in the Vertebrata. *Roy. Soc. London*, 237 pp.

PETRONIEVICS, B. 1918. Pectoral fin of *Eusthenopteron*. *Ann. Mag. Nat. Hist.*, ser. 9, vol. 2, pp. 471–476.

POLLARD, H. B. 1892. On the anatomy and phylogenetic position of *Polypterus*. *Zool. Jahrb.*, Bd. 5, pp. 387–428.

PYCHLAU, W. 1908. Untersuchungen an den Brustflossen einiger Teleostier. *Jenaische Zeitschr. Nat.*, Bd. 43, pp. 692–728.

RABL, C. 1901. Gedanken und Studien über den Ursprung der Extremitäten. *Zeitschr. wiss. Zool.*, Bd. 70, Heft 3, pp. 474–558.

REGAN, C. T. 1904. Phylogeny of Teleostomi. *Ann. Mag. Nat. Hist.*, ser. 7, vol. 13, pp. 328–349.

ROMER, A. S. 1924. Pectoral limb musculature and shoulder-girdle structure in fish and tetrapods. *Anat. Rec.*, vol. 27, pp. 119–143.

SABATIER, A. 1880. Comparaison des ceintures et des membres antérieurs et postérieurs dans la série des vertébrés. *Montpellier*, 455 pp.

SEWERTZOFF, A. N. 1908. Studien über die Entwickelung der Muskeln, Nerven und des Skeletts der Extremitäten der niederen Tetrapoda. *Bull. Soc. Imp. Nat. Moscou*, vol. 21, pp. 1–430.

SEWERTZOFF, A. N. 1926. Die Morphologie der Brustflossen der Fische. *Jenaische Zeitschr. Naturw.*, Bd. 62, pp. 341–392.

SHANN, E. W. 1920. The comparative myology of the shoulder-girdle and pectoral fin in fishes. *Trans. Roy. Soc. Edinburgh*, vol. 52, pt. 3, pp. 531–570.

———. 1924. Further observations on the myology of the pectoral region in fishes. *Proc. Zool. Soc. London*, pp. 195–215.

SHERRINGTON, C. S. 1920. The Integrative Action of the Nervous System. Yale Univ. Press, 411 pp.

STENSIÖ, E. A. 1927. The Downtonian and Devonian vertebrates of Spitzbergen. Part 1. Family Cephalaspidae. *Det. Norske Videnskaps-Akad.* I Oslo, pp. 391.

SWINNERTON, H. 1906. A contribution to the morphology and development of the pectoral skeleton of teleosteans. *Quart. Jour. Micros. Sci.*, vol. 49, pp. 363–382.

THACHER, J. K. 1877. Median and paired fins, a contribution to the history of vertebrate limbs. *Trans. Conn. Acad.*, vol. 3, pp. 281–310.

VETTER, B. 1874. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermusculatur der Fische. *Jenaische Zeitsch. Naturw.* Bd. 8, pp. 405–458.

———. 1878. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermusculatur der Fische. *Jenaische Zeitschr. Naturw.*, Bd. 12, pp. 431–550.

WATSON, D. M. S. 1918. The evolution of the tetrapod shoulder girdle and fore-limb. *Jour. Anat.*, vol. 52, pp. 1–63.

WIEDERSHEIM, R. 1892. Das Gliedmaassenskelet der Wirbelthiere mit besonderer Berücksichtigung des Schulter- und Beckengürtels bei Fischen, Amphibien und Reptilien. *Jena.*

———. 1902. Vergleichende Anatomie der Wirbelthiere. *Jena.*

THE FUNCTIONAL COMPONENTS OF THE DORSAL ROOTS OF SPINAL NERVES

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THERE has been considerable dispute in regard to the allocation of credit for elucidation and physiological demonstration of the law of the roots (Fulton, '30, pp. 251 and 258). Likewise the validity of this law has been challenged and questioned in relation to both the dorsal and ventral roots. It has been suggested that, in addition to carrying afferent impulses to the spinal cord, the dorsal roots serve as pathways for efferent impulses to skeletal muscle, blood vessels, other viscera and the sweat glands, the so-called spinal parasympathetic pathways. The evidence for and against such conduction to skeletal muscle has been reviewed by Ranson ('29). There is no question but that stimulation of the dorsal roots produces vasodilatation but the evidence which Bayliss ('02), and Fofanow and Tschalussow ('13) presented for antidromic reflex conduction has not been accepted (Hinsey, '28; Hinsey and Gasser, '30). The literature concerning an inhibitory action on sweat secretion mediated by the dorsal roots is considered by Müller ('29).

If there is any efferent conduction over the dorsal roots, it must be subserved in one of two ways. The ordinary sensory fibers may conduct antidromically with reversal of the polarity of the synapse in the central gray matter (Kohnstamm, '00). On the other hand, fibers may arise in the spinal cord and pass either to a synaptic junction in the dorsal root ganglion or directly through the ganglion to reach the site of their physiologic action. It is with these fibers of intraspinal origin that we are concerned in this review.

The difference in results from similar experimental procedures upon this problem is merely an expression of the many pitfalls which await the experimental neurologist, who oftentimes fails to recognize the fact that the methods at his disposal are not as infallible as he may deem them to be. A consideration of the phylogeny and ontogeny of the nervous system is extremely valuable in the interpretation of experimental methods. For this reason, it has been thought worth while to consider the fiber content of the dorsal roots from a comparative point of view. While a complete treatment is beyond the bounds of this communication, an endeavor will be made to give a summary of some of the important contributions. A detailed account is given by Kappers ('20). In considering the content of the dorsal roots of the different vertebrates, it is important to remember that there may be present afferent fibers (both somatic and visceral) with cells of origin in the dorsal root ganglia, afferent fibers with cells of origin within the spinal cord, and visceral efferent and somatic efferent ones of intramedullary origin.

THE LOWER VERTEBRATES

In *Amphioxus*, a part of the sensory ganglion cells is found within the spinal cord in the hypothetical primitive position for vertebrates; while most of them have progressed somewhat toward the periphery and are found scattered along the

dorsal root even beyond its division into dorsal and ventral rami (Johnston, '05). Although the latter are not grouped into an extramedullary spinal ganglion, they may be thought to occupy a position which is typical for the higher vertebrates. Visceromotor fibers traverse the dorsal roots instead of the ventral ones, which are made up of somatic motor fibers.

An extramedullary spinal ganglion is present in *Petromyzon*. Intramedullary sensory ganglion cells have been denied by Tretjakoff ('09), but they are said to be present by Kolmer ('05) and Beccari ('09). The majority of the visceromotor fibers course in the dorsal roots and it is possible that a few may be present in the ventral ones.

The dorsal and ventral roots join in the Elasmobranchs and course in mixed nerves in contrast to the failure of union of these roots seen in *Amphioxus* and *Petromyzon*. In the adults, all sensory cells are located in an extramedullary spinal ganglion. The embryos, however, possess intramedullary sensory cells found in the dorsal median portion of the spinal cord. These are found only in larval stages and send peripheral branches to the skin and to skeletal muscle. Their development, structure and disappearance were described by Beard ('92, '96). Just as in the Amphibia, these Rohon ('84)—Beard cells disappear during larval life; they do not move out to the spinal ganglia. The visceromotor fibers course through the posterior roots. It is not definitely known whether or not some of these visceral efferent fibers make their exit from the spinal cord over the ventral roots.

In the bony fishes, the sensory fibers have their cells of origin in extramedullary spinal ganglia as well as from cells within and above the spinal cord. These intra- and supramedullary sensory ganglion cells are present not only in the larvae but persist in the adult forms (Kappers, '20, p. 138). Visceral efferent fibers pass out over both the dorsal and ventral roots.

AMPHIBIANS AND REPTILES

Considerable work has been done on the anatomy and physiology of the dorsal roots in the Amphibia. In the larval stages Rohon-Beard cells are present. Fundamental studies have been made upon them in the correlation of their structure and function by Coghill ('14, '29) and by Herrick and Coghill ('15). However, in the adult forms these intramedullary sensory cells have disappeared and extramedullary spinal ganglia are present. The ventral roots contain somatic motor and visceral motor fibers. Steinach and Wiener ('95) and Steinach ('98) believed there were dorsal root motor fibers for the oesophagus, stomach, rectum and bladder. Horton-Smith ('97) was unable to confirm this for the viscera, but he did find somatic motor fibers in the dorsal roots in a limited number of cases. In seven of twelve hundred dorsal roots, Wana ('98) found somatic motor fibers to the skeletal muscles of the hind limb in the frog. Dale ('02) obtained contraction of certain skeletal muscles in three of twelve cases with *Rana temporaria* but there was no trace of this effect in ten experiments upon the toad. He did not elicit any visceromotor effects from the 6–7–8–9–10 dorsal roots. He sectioned these roots between the ganglia and the cord and allowed seventeen, thirty, thirty-seven, and forty-nine days degeneration. In the peripheral cut ends, he did not find a single fiber showing any sign of degeneration. In the proximal stumps of the dorsal roots, the myelinated fibers followed the Wallerian law of degeneration; furthermore, methylene blue preparations failed to reveal any unmyelinated fibers of intraspinal origin in these

proximal stumps. After an investigation of the autonomic system in the frog, Langley and Orbeli ('10) believed that the presence of visceral efferent fibers in the posterior roots was a rare phenomenon and not a normal distribution. Elze ('23), after section of the dorsal roots in frogs and toads, saw degenerating fibers in the peripheral stump and intact ones in the central portion of the roots.

In adult reptiles, the sensory ganglion cells for the spinal nerves are located in the dorsal root ganglia. The ventral roots contain somatic motor and visceromotor fibers. It cannot be said with certainty whether or not a few visceral efferent fibers course in the dorsal roots. In the cervical segments of lizard embryos, Beccari ('14) found cells in the medial portion of the ventral horn whose fibers passed out to join the dorsal roots by way of separate filaments of exit, slightly ventral to the dorsal roots proper. These cells are typical motor cells and resemble the somatic motor cells in the anterior horn. The peripheral destination of these fibers has not been shown, any more than that they join with fibers of the dorsal roots. Banchi ('03) saw these cells in the cervical cord of the turtle. Van Gehuchten ('96) failed to find them in the embryos of the snake *Tropidonotus natrix*. His observations confirmed those of Retzius ('94).

BIRDS

The afferent fibers all arise from extramedullary dorsal root ganglia in the spinal nerves of birds. The visceral and somatic efferent fibers leave the cord by way of the ventral roots. However, motor posterior root fibers have been described in the spinal cord of chick embryos. These posterior radicular cells of von Lenhossék are situated in the medial and lateral portions of the anterior horn and are said by Kappers ('20) to be present only in the cervical segments. The axones pass dorsally to make their exit in the posterior roots and they have not been traced beyond the ganglion. These have been described by von Lenhossék ('90) in chick embryos of four and five days incubation, by Cajal in those of five and six days ('90) and fifty-six hours ('08), by Van Gehuchten ('93) in those of eleven days, by Martin ('95) in twelve day embryos and by Tello ('22) in three and four day embryos. They are large multipolar cells resembling somatic motor ones. Their functional interpretation has never been made with certainty. Although the majority of the visceral efferent fibers leave the spinal cord by way of the ventral roots, perhaps these posterior root motor fibers should be considered as visceral efferent. Their situation in the cervical cord of reptiles and birds led Beccari ('14) to suppose that they are the forerunners of the spinal accessory nerve. In grown mammals where the spinal accessory is derived from the cervical segments, they are found in the accessory rootlets instead of in the dorsal roots. Thus they may represent somatic motor fibers which pass out over the dorsal roots instead of over the customary path in the ventral ones. Proof is certainly not present that these fibers are anything else than motor fibers to skeletal muscle. However, in the absence of definite evidence to the contrary, it must be admitted that there may be visceral efferent fibers in the dorsal roots not only in the cervical segments but in other portions of the spinal cord of birds.

MAMMALS

In the spinal nerves of mammals, the sensory fibers, both somatic and visceral, have their cells of origin in the dorsal root ganglia. The somatic and visceral efferent fibers, with cells of origin in the central gray, course in the ventral roots.

Exceptions to this fundamental type of architecture are found in the cranial nerves where some of the sensory cells of origin are found within the brain stem, i.e. the nucleus of the mesencephalic root of the trigeminal nerve. Numerous experiments have seemed to indicate that there are to be found fibers with cells of origin within the spinal gray passing out over the dorsal roots of spinal nerves.

In some of Waller's ('52) early experiments on the second cervical dorsal roots, he found that a very few normal looking fibers remained among the degenerating ones ten to fifteen days after section of the dorsal root between the ganglion and the cord. In other animals, he performed the important experiment of sectioning the 2 C dorsal root on one side and removing the spinal ganglion on the other. Two months later, he observed that all of the fibers in the proximal stumps on both sides were degenerated. In unstained preparations, he saw regenerating fibers which he recognized as such both on the side where the ganglion was present and on the side where it had been extirpated. While Waller is known for the law of degeneration, some of his observations on unstained material with degeneration methods were remarkably accurate.

The work of Joseph ('87), which was at first controverted and then later confirmed by Singer and Münzer ('95), showed that, following section of the dorsal roots, degenerating fibers were seen in the peripheral stump and intact ones in the central stump of the cat. Mott ('90) sectioned dorsal roots in two monkeys and allowed thirty days degeneration time. He says, "In the lower lumbar and upper sacral segments corresponding to the roots divided, there is complete degeneration of all fibres entering the posterior horn." Sherrington ('94) found minute myelinated fibers in the proximal stumps of the dorsal roots in the lumbosacral region of the cat, five weeks after excision of the ganglia and section of both the dorsal and ventral roots. In the course of the second and third weeks, he was unable to find them. He considered the possibility that these were regenerating fibers, but inasmuch as the sensory ganglia had been excised, he did not know where to look for their origin. He did not consider the possibility that they had regenerated from the proximal stumps of the ventral roots. In a later paper ('97), he extended this work on both the cat and monkey to the segments of the spinal cord giving rise to the thoracolumbar visceral efferent fibers. He concluded that none of the fibers in the dorsal root arise in intraspinal nerve cells. Due to the fact that his method was of such nature that he observed and measured myelinated fibers of diameters from 1 to 3.5μ, it is certain that he would have seen the smallest of them. While Kölliker ('96) was able to confirm the presence of dorsal root efferent fibers in the chick embryo, a thorough search failed to reveal any such fibers in mammals including man. Similar conclusions were reached from experimental procedures by Gabri ('96, in the lumbosacral region of the dog), Van Gehuchten ('00, lumbar region of the dog), Bikeles ('03, dog), Kopczynski ('06, cervical and upper thoracic regions of the monkey), and Lapinsky ('07, dog).

On the other hand, Morat and Bonne ('97) thought they had evidence for the presence of efferent vasomotor fibers in the 6-7 L and 1 S dorsal roots of the dog. They sectioned the dorsal roots proximal to the ganglion, allowed various intervals from eight to 106 days, and stained with osmic acid. Lugaro ('06) found a certain number of unmyelinated centrifugal fibers in the posterior roots, three months or more after section and removal of the

ganglia in the dog. In preparations stained with the Cajal method, he recognized the presence of regenerating fibers, but he thought that, in addition to the regenerating fibers, there were also some efferent ones. Timasheff ('11) cut lumbar dorsal roots in dogs. Following three to fifteen days' degeneration, he examined the distal portion of the roots and their attachment to the spinal ganglia in preparations stained with the Marchi as well as other methods. About five per cent of the fibers underwent degeneration. The gray matter of the same, and to some extent that of the opposite, side in the corresponding segments showed chromatolysis in some of the cells in the anterior and lateral portions of the ventral horns.

In the course of experiments on the tract of Lissauer and the dorsal roots, Ranson ('14) made some observations on the proximal stumps of ligated and cut dorsal roots without removal of the ganglia in the lumbosacral region of the cat. These observations were reviewed by Ranson ('29). His preparations were stained with Pal-Weigert, Marchi, and pyridine silver. He says, "In none of these have I ever seen any clear-cut evidence of efferent dorsal root fibers." He is of the opinion that the unmyelinated fibers which he found in the degenerated roots can be explained only on the basis of regeneration, but he feels that the possibility could not be excluded that the fine fibers seen entering the cord may have had their cells of origin in the cord.

After excision of the dorsal root ganglia in the lumbosacral region of dogs, Nevin ('30) stained the proximal and distal portions of the roots with osmic acid and pyridine silver. His observations were negative as to the presence of efferent fibers in the dorsal roots. Tower ('31) excised the dorsal root ganglia supplying the brachial plexus in cats. After six months to a year, unmyelinated and small myelinated fibers were present in the proximal stumps. These were shown to be regenerating fibers from the ventral roots. Their entry into the posterior horn of the cord was atypical and unlike the normal distribution. Her observations supported the conclusion that there were no fibers of intraspinal origin in the dorsal roots.

Kuré ('31) has brought together the observations which he and his co-workers ('28, '30) have made on this subject. After thirteen to 103 days, many fine myelinated as well as some larger fibers (Weigert method) were found in the central stumps of divided roots in dogs. They believe that as many as forty per cent of the fibers in the dorsal root may have an intraspinal origin in the posterior gray matter. These "spinal parasympathetic fibers" are said to pass out over the dorsal roots to terminate in the spinal ganglia. The presence of chromatolysis in the gray matter of the posterior horn following dorsal root section convinced them that the cells of origin were to be found here. This chromatolysis might have been due to anemia inasmuch as section of the posterior roots also severs the blood vessels accompanying them. The spinal ganglia were not excised and the probability of regeneration was certainly not removed by the methods they employed. Furthermore, in the shorter degeneration intervals they used, incomplete degeneration must be considered. In failing to study the entrance of the roots into the spinal cord in properly stained material instead of the cross sections of the proximal stumps, they have fallen short of the proof required for the establishment of the intraspinal origin of the fibers they describe. Gagel ('30) confirmed Kuré in eight cases in which Foerster sectioned human sensory roots

for therapeutic reasons. Although Gagel studied some sections at the root entrance zone, he did not trace the fibers into the spinal cord. Regeneration could not be ruled out in his cases. Recently Okelberry ('32) has stated that there is a considerable number of large and medium sized as well as small fibers of an efferent nature in the dorsal roots of the lumbar region in dogs.

O'Leary, Heinbecker and Bishop ('32) found regenerating fibers in pyridine silver preparations of the central stumps of dorsal roots 20 to 25 days after section and crushing proximal to the dorsal root ganglion in the cat. However when the dorsal root ganglia were removed in three successive segments and adequate degeneration time was allowed, evidence of the occurrence of intact fibers, either myelinated or unmyelinated, was lacking. They concluded that both the small myelinated and unmyelinated fibers of the dorsal roots have their cells of origin in the dorsal root ganglia.

Hinsey ('31 and '33) has presented experimental evidence that negates the occurrence of dorsal root efferent fibers in the cervical, lower thoracic and upper lumbar, and the lumbosacral segments of the cat. This is based upon absence of peripheral degeneration as shown by the Marchi method following section of the dorsal roots proximal to the ganglia and upon the absence of axones in the proximal stumps and at the root entrance zone (pyridine silver method) following removal of the sensory ganglia. Attention was called to the errors of interpretation which may result from incomplete degeneration at the root entrance zone and from regeneration even after removal of the ganglia (Cajal, 1928).

There is no indication from comparative neurological studies which would point definitely to cells of intraspinal origin in the dorsal roots of mammals, either of an afferent or visceral efferent character. There is no conclusive proof of an experimental nature which will withstand critical examination. The work of Windle ('32), based upon an examination of serial sections of early cat embryos, demonstrates the absence of such fibers in mammalian ontogeny. That Sherrington has not deviated from his original view-point is shown by the following statement, "There is no convincing evidence that in mammals the dorsal spinal roots contain any fibres having their cells of origin elsewhere than in the root ganglion; that is, the dorsal roots contain no fibres arising within the central nervous system." (Creed, Denny-Brown, Eccles, Liddell and Sherrington, '32.) As far as the morphological evidence goes, the law of the roots still seems to be valid when it is applied to the dorsal roots of mammalian spinal nerves.

LIST OF LITERATURE

Banchi, A. 1903. La minuta struttura della midolla spinale dei Chelonii (*Emys europaea*). *Arch. Ital. d. Anat. e di Embriol.*, vol. 2, pp. 291–307.

Bayliss, W. M. 1902. Further researches on antidromic nerve impulses. *Jour. Physiol.*, vol. 28, pp. 276–299.

Beard, J. 1892. The transient ganglion cells and their nerves in *Raja batis*. *Anat. Anz.*, vol. 7, pp. 191–206.

———. 1896. The history of a transient nervous apparatus in certain Ichthyopsida. An account of the development and degeneration of ganglion cells and nerve fibers. *Zool. Jahrbuch*, vol. 9, pp. 319–426.

Beccari, N. 1909. Le cellule dorsali o posteriori dei ciclostomi. *Monit. Zool. Ital.*, vol. 20, (quoted from Kappers, 1920).

———. 1914. II, IX, X, XI e XII pajo di nervi cranici e i nervi cervicali negli embrioni di *Lacerta muralis*. *Arch. Ital. d. Anat. e di Embriol.*, vol. 13, pp. 1–78.

Bikeles, G. 1903. Anatomische Befunde nach Durchquetschung von Rückenmarkswurzeln beim Hunde. *Neurol. Centralbl.*, vol. 22, pp. 248–253.

CAJAL, S. RAMON Y. 1890. Sur l'origine et les ramifications des fibres nerveuses de la moelle embryonnaire. *Anat. Anz.*, vol. 5, pp. 85–95.

———. 1890. À quelle époque apparaissent les expansions des cellules nerveuses de la moelle épinière du poulet? *Anat. Anz.*, vol. 5, pp. 631–639.

———. 1908. Nouvelles observations sur l'évolution des neuroblasts, avec quelques remarques sur l'hypothèse neurogénétique de Hensen-Held. *Anat. Anz.*, vol. 32, pp. 1–25; 65–87.

———. 1928. Degeneration and Regeneration of the Nervous System. Translated by R. M. May. *London*, Oxford University Press. Vols. 1 and 2.

COGHILL, G. E. 1914. Correlated anatomical and physiological studies of the growth of the nervous system of the trunk of *Amblystoma*. *Jour. Comp. Neurol.*, vol. 24, pp. 161–233.

———. 1929. Anatomy and the Problem of Behavior. *New York*, Macmillan.

CREED, R. S., D. DENNY-BROWN, J. C. ECCLES, E. G. T. LIDDELL and C. S. SHERRINGTON. 1932. Reflex Activity of the Spinal Cord. *London*, Oxford Press.

DALE, H. H. 1901/02. Observations chiefly by the degeneration method on possible fibres in the dorsal nerve roots of the toad and frog. *Jour. Physiol.*, vol. 27, pp. 350–355.

ELZE, C. 1923. Untersuchungen am sympathischen Nervensystem. *Pflüger's Arch.*, vol. 198, pp. 349–358.

FOFANOW, L. D., and M. A. TSCHALUSSOW. 1913. Über die Beziehungen des N. depressor zu den vasomotorischen Zentren. *Pflüger's Arch.*, vol. 151, pp. 543–582.

FULTON, J. F. 1930. Selected Readings in the History of Physiology. *Springfield*, C. C. Thomas.

GABRI, G. 1896. À propos des cellules radiculaires postérieures de v. Lenhossek et Ramon y Cajal. *Arch. Ital. d. Biol.*, vol. 26, pp. 115–119.

GAGEL, O. 1930. Zur Frage der Existenz efferenter Fasern in den hinteren Wurzeln des Menschen. *Zeitschr. f. d. ges. Neurol. u. Psychiat.*, vol. 126, pp. 405–416.

GEHUCHTEN, A. VAN. 1893. Les éléments nerveux moteurs des racines postérieurs. *Anat. Anz.*, vol. 8, pp. 215–223.

———. 1896. Contribution à l'étude de la moelle épinière chez les vertébrés (*Tropidonotus natrix*). *La Cellule*, vol. 12, pp. 115–165.

———. 1900. Anatomie du Système Nerveux de l'Homme. *Louvain*. 3rd Edition.

———. 1903. La dégénérescence dite rétrograde ou dégénérescence Wallérienne indirecte. *Le Névraxe*, vol. 5, pp. 1–107.

HERRICK, C. J., and G. E. COGHILL. 1915. The development of reflex mechanisms in *Amblystoma*. *Jour. Comp. Neurol.*, vol. 25, pp. 65–85.

HINSEY, J. C. 1928. Observations on the innervation of the blood vessels in skeletal muscle. *Jour. Comp. Neurol.*, vol. 47, pp. 23–65.

———. 1931. Degeneration studies upon dorsal roots in cats. *Anat. Rec.*, vol. 48, p. 48 (abstract).

———. 1934. Are there efferent fibers in the dorsal roots? *Jour. Comp. Neurol.*, (in press). Feb. 1934.

HINSEY, J. C., and H. S. GASSER. 1930. The component of the dorsal root mediating vasodilatation and the Sherrington contracture. *Amer. Jour. Physiol.*, vol. 92, pp. 679–689.

HORTON-SMITH, R. J. 1897. On efferent fibres in the posterior roots of the frog. *Jour. Physiol.*, vol. 21, pp. 101–111.

JOHNSTON, J. B. 1905. The cranial and spinal ganglia and the visceromotor roots in *Amphioxus*. *Biol. Bull.*, vol. 9, pp. 112–127.

JOSEPH, M. 1887. Zur Physiologie der Spinalganglien. *Arch. f. (Anat. u.) Physiol.*, pp. 296–315.

KAPPERS, C. U. A. 1920. Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen. *Haarlem*, Erven F. Bohn. Vols. 1 and 2.

KOHNSTAMM, O. 1900. Zur Theorie des Reflexes von hinterer Wurzel auf hintere Wurzel. *Centralbl. f. Physiol.*, vol. 14, pp. 458–459.

KÖLLIKER, A. 1896. Handbuch der Gewebelehre des Menschen. Bd. 2. Nervensystem des Menschen und der Thiere. *Leipzig*, W. Engelmann.

KOLMER, W. 1905. Zur Kenntnis des Rückenmarkes von *Ammocoetes*. *Anat. Hefte*, vol. 29, pp. 163–214.

KOPCZYNSKI, S. 1906. Experimentelle Untersuchungen aus dem Gebiete der Anatomie und Physiologie der hinteren Spinalwurzeln. *Neurol. Centralbl.*, vol. 25, pp. 297–300.

KURÉ, K., Y. NITTA, M. TUZI, K. SIRAISI, and B. SUYENAGE. 1928. Demonstration of special parasympathetic nerve-fibres in the dorsal or posterior roots of the lumbar region of the spinal cord. *Quart. Jour. Exp. Physiol.*, vol. 18, pp. 333–344.

KURÉ, K., G. SAEGUSA, K. KAWAGUCHI, and K. SHIRAISHI. 1930. On the parasympathetic (spinal parasympathetic) fibres in the dorsal roots and their cells of origin in the spinal cord. *Quart. Jour. Exp. Physiol.*, vol. 20, pp. 51–66.

KURÉ, K. 1931. Über den Spinal-Parasympathikus. *Basel*, B. Schwabe & Co.

LANGLEY, J. N., and L. A. ORBELI. 1910. Observations on the sympathetic and sacral autonomic system of the frog. *Jour. Physiol.*, vol. 41, pp. 450–482.

LENHOSSÉK, M. VON. 1890. Über Nervenfasern in den hinteren Wurzeln welche aus dem Vorderhirn entspringen. *Anat. Anz.*, vol. 5, pp. 360–362.

LAPINSKY, M. 1907. Zur Frage der Ursachen der motorischen Störungen bei Läsionen der hinteren Wurzeln und des Verlaufes der Collateralen im Rückenmark. *Arch. f. Psychiat. u. Nervenkrankh.*, vol. 42, pp. 869–899.

LUGARO, E. 1906. Fibre aberranti, fibre centrifughe e fibre ricorrenti nelle radici posteriori. *Monit. Zool. Ital.*, vol. 17, pp. 217–220.

MARTIN, I. 1895. Contribution à l'étude de la structure interne de la moelle épinière chez le poulet et chez la truite. *La Cellule*, vol. 11, pp. 55–83.

MORAT, J. P., and C. BONNE. 1897. Les éléments centrifuges des racines postérieures médullaires. *Comp. Rend. de l'Acad. d. Sci.*, vol. 125, pp. 126–128.

MOTT, F. W. 1890. The bipolar cells of the spinal cord and their connections. *Brain*, vol. 13, pp. 433–448.

MÜLLER, L. R. 1929. Über die Gegensätzlichkeit in der Lebensinnervation. *Deutsche Zeitschr. f. Nervenheilk.*, vol. 111, pp. 102–110.

NEVIN, S. 1930. Degeneration changes after unilateral lumbar sympathectomy, with general observations on the nerve fibre constitution of peripheral nerves and nerve roots. *Quart. Jour. Exp. Physiol.*, vol. 20, pp. 281–297.

OKELBERRY, A. M. 1932. Demonstration of dorsal root efferent fibers in the dog. *Anat. Rec.*, vol. 52, p. 72 (abstract).

O'LEARY, J. L., P. HEINBECKER and G. H. BISHOP. 1932. Dorsal root fibers which contribute to the tract of Lissauer. *Proc. Exp. Biol. and Med.*, vol. 30, pp. 302–303.

RANSON, S. W. 1914. An experimental study of Lissauer's tract and the dorsal roots. *Jour. Comp. Neurol.*, vol. 24, pp. 531–545.

———. 1929. The parasympathetic control of muscle tonus. *Arch. Neurol. and Psychiat*, vol. 22, pp. 265–281.

RETZIUS, G. 1894. Die embryonale Entwicklung der Rückenmarkselemente bei den Ophidiern. *Biolog. Untersuchung.*, vol. 6, pp. 41–45.

ROHON, V. 1884. Zur Histogenese des Rückenmarks der Forelle. *Sitzungsberichte Ak. Wien.*, pp. 39–57. (Not seen.)

SHERRINGTON, C. S. 1894. On the anatomical constitution of nerves. *Jour. Physiol.*, vol. 17, pp. 211–258.

———. 1897. On the question of whether any fibres of the mammalian dorsal (afferent) spinal root are of intraspinal origin. *Jour. Physiol.*, vol. 21, pp. 209–212.

SINGER, J., and E. MÜNZER. 1895. Beiträge zur Anatomie des Centralnervensystems. *Denkschr. d. k. Akad. d. Wissensch., Mathnaturw. Klasse, Wien.*, vol. 57. (Not seen.)

STEINACH, E., and H. WIENER. 1895. Motorische Funktionen hinterer Spinalnervenwurzeln. *Pflüger's Arch.*, vol. 60, pp. 593–622.

STEINACH, E. 1898. Über die viscero-motorische Funktionen. *Pflüger's Arch.*, vol. 71, pp. 523–554.

TELLO, J. F. 1922. Les différenciations neuronales dans l'embryon du poulet, pendant les premiers jours de l'incubation. *Trav. Lab. Rech. Biol. Univ. Madrid*, T. 21, pp. 1–93.

TIMASHEFF, N. K. 1911. Nevrol. Vestnik. 18, pp. 777. (Original not seen. There is a translation at the Institute of Neurology at Northwestern University.)

TOWER, S. S. 1931. A search for trophic influence of posterior spinal roots on skeletal muscle, with a note on the nerve fibres found in the proximal stumps of the roots after excision of the root ganglia. *Brain*, vol. 54, pp. 99–111.

TRETJAKOFF, D. 1909. Das Nervensystem von *Ammocoetes*. 1. Rückenmark. *Arch. f. mikroskop. Anat.*, vol. 73, pp. 607–680.

WALLER, A. 1852. Recherches expérimentales sur la structure et les tonctions des ganglions. *Compt. rend. de l'Acad. des Sciences*, vol. 34, pp. 524–527.

———. 1852. Examen des altérations qui ont lieu dans les filets d'origine du nerf pneumo-gastrique et des nerfs rachidiens, par suite de la section de ces nerfs au-dessus de leurs ganglions. *Compt. rend. de l'Acad. des Sciences*, vol. 34, pp. 842–847.

WANA, J. 1898. Über abnormen Verlauf einzelner motorischer Nervenfasern im Wurzelgebiet. *Pflüger's Arch.*, vol. 71, pp. 555–559.

WINDLE, W. F. 1932. The neurofibrillar structure of the 7 mm. cat embryo. *Jour. Comp. Neurol.*, vol. 55, pp. 99–138.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE MEANING OF ANIMAL COLOUR AND ADORNMENT. *Being a New Explanation of the Colours, Adornments and Courtships of Animals, Their Songs, Moults, Extravagant Weapons, the Differences Between Their Sexes, the Manner of Formation of Their Geographical Varieties, and Other Allied Problems.*

By R. W. G. Hingston. Longmans, Green and Co., New York. $6.00. $5\frac{3}{8}$ x $8\frac{7}{8}$; 411; 1933.

Major Hingston, a distinguished naturalist whose earlier books have been reviewed in these columns, presents to his readers an extensive array of facts concerning color and adornment in animals to support his *color-conflict* theory. This theory is that animals, broadly speaking, possess two dominating emotions, fear and anger, balanced, as it were, against one another. These emotions are represented on their exteriors by two opposing patterns of colour, one concealing and the other threatening. If at any moment fear predominates, then the concealing pattern will predominate in the colour-scheme and the animal will blend more closely with its environment. If, on the other hand, anger predominates, then the threatening element will predominate in the pattern and the animal will appear less like its environment.

As a concrete illustration the author uses the lion, whose tawny coat harmonizes well with the khaki plains on which it lives. When angered the lion brings his intimidating machinery into action. He spreads his mane, throwing an area of black around his head and neck; he throws his tail (at the end of which is a brush of blackish hairs) above his back and draws back and rotates his ears, bringing dark patches directly forward. The intensity of his emotions is indicated by the degree in which he renders his threatening colors conspicuous to his foe. Extending this theory to many types of mammals and lower animals, the author finds that it applies in the explanation of courtship, songs, extravagant weapons, the formation of geographical varieties and allied problems. Major Hingston's philosophical ideas concerning the meaning of color merit the careful attention of biologists.

The book contains much about the habits of animals that will be of interest to the general reader. It is well illustrated with drawings by the author, and is indexed.

VERTEBRATE PALEONTOLOGY.

By Alfred S. Romer. University of Chicago Press, Chicago. $5.00. $6\frac{3}{4}$ x $9\frac{3}{4}$; vii + 491; 1933.

A useful reference book for biological laboratories and an excellent textbook for paleontological courses. The material is arranged as a group-by-group treatment of the vertebrates, the various ramifications of the family tree being traced out. Major structural features of each group are described in considerable detail. The work concludes with a synoptic classification of vertebrates, a bibliography of 314 titles and brief historical notes, and an index. There are 359 figures in the text.

GENETICS

INHERITED ABNORMALITIES OF THE SKIN AND ITS APPENDAGES.

By E. A. Cockayne. Oxford University Press, New York. $8.00. 5½ x 8⅝; x + 394; 1933.

This book will be of great usefulness to those dermatologists who are interested in following up the genetics of skin abnormalities which come under their observation. An introductory chapter deals clearly and concisely with Mendelian inheritance. In the fourteen chapters following, widely diverse disorders are discussed, many of which are not primarily defects of the skin and its appendages but are obvious in the ectodermal structure. The work should lead to a wider interest in the recording of pedigrees and reports of families in which such defects are inherited. Geneticists will find many suggestions in the data given for profitable future lines of work. Many diagrams and tables are included in the text. The documentation and indexing are excellent.

DAS PERSÖNLICHE TEMPO. *Eine erbbiologische Untersuchung. Sammlung psychiatrischer und neurologischer Einzeldarstellungen, Band IV.*

By Ida Frischeisen-Köhler. Georg Thieme, Leipzig. 5.50 marks. 6¾ x 10; 63; 1933 (paper).

An individual has a fairly definite rhythm of tapping with a finger on a table or of patting on the floor with his foot, and there are clearly marked individual preferences for certain metronome rhythms. These tempos are so constant that they may be used as genetic characteristics, we are told; they are alleged not to vary in different age groups or in different social classes. Women go in for slightly faster rhythms than men. Identical twins show less variation in tempo than fraternal twins.

MULTIPLE SKLEROSE UND ERBANLAGE.

By Friedrich Curtius. Georg Thieme, Leipzig. 18 marks (paper); 20 marks (cloth). 6¾ x 10; 215; 1933.

A noteworthy contribution to the literature on the constitutional factor in multiple sclerosis. Many case histories and pedigree charts are given, including data on the age of onset of various symptoms in the members of each family suffering from this disease. Suggestions are made for further study of etiological factors in this malady. The book is provided with a bibliography of eleven pages, but has no index.

GENERAL BIOLOGY

SÉNILITÉ ET RAJEUNISSEMENT.

By Auguste Lumière, J. -B. Baillière et Fils, Paris. 18 francs. 5⅜ x 8¼; 160; 1932 (paper).

In the earlier chapters of this book the author gives a short treatment of his thesis elaborated fully in his *La Vie, La Maladie et La Mort*, noticed in Volume 4 of this REVIEW, namely, that the colloidal state is a necessary condition of life, and that sickness and death result from the destruction of this state. In the chapters on senility he advances his theory that senescence results from the evolution of the colloids and micelloids toward destruction by precipitation or flocculation. Theoretically this destruction should begin at the same age in all individuals of the same species, but infinitely variable external factors may, and do, hasten the destruction. In this connection he moralizes a little in the *modicus cibi, medicus sibi* vein. The last chapter contains a review of the work of Steinach, Voronoff, and others on rejuvenescence from which the author concludes that:

> In reality, the old colloids are not modified by means of extracts of genital glands, but these latter produce an excitation of the cells which provokes their multiplication. It causes new cells and consequently new colloids and micelloids which are the cause of the phenomenon of rejuvenescence, more or less appreciable and always temporary.

A bibliography is provided.

URZEUGUNG UND LEBENSKRAFT. *Zur Geschichte dieser Probleme von den ältesten Zeiten an bis zu den Anfängen des 20. Jahrhunderts.*

By Edmund O. von Lippmann. Julius Springer, Berlin. 9.60 marks. 6⅜ x 9½; viii + 135; 1933 (paper).

The eminent historian of chemistry relates to us the history of the problem of the origin of organisms, from the earliest times down to the beginning of the twentieth century. The problem is one that has always busied and baffled the human mind, and the record of the various hypotheses proposed for its solution shows the same conflict between mechanism and vitalism ever emerging during the course of the centuries, though under different forms or names and remaining in part unchanged in our own times. The author reaches the conclusion that the problem of the nature and origin of life cannot be solved on the basis of natural science alone but belongs ultimately to metaphysics. The story is told in a manner that will appeal not only to scientists, physicians, and philosophers, but to the educated in general as well. No *Fachkenntnis* is required.

Three indices—names of authors and anonymous works; geographical and proper names; topical index—give the book a special value as a work of reference.

MODERN THEORIES OF DEVELOPMENT. *An Introduction to Theoretical Biology.* *By Ludwig von Bertalanffy. Translated and adapted by J. H. Woodger. Oxford University Press, New York.* $2.50. 5 x 7½; x + 204; 1933.

Professor Woodger has done an excellent piece of work in the translation and adaptation for English readers of this important contribution to the philosophy of biology. To the original German edition have been added the results of such investigations as have appeared since its publication. The book is not a summary of investigations on the physiology of development, but is an attempt to show "a way to a new organization of biology which, we believe, will permit the present difficulties and contradictions—or at least many of them—to be overcome." The principal current theories are described and critically evaluated. Those experimental results which are most essential from the theoretical standpoint are described. The translating has been done with great skill. There is a bibliography and an author and subject index.

THE LAMARCK MANUSCRIPTS AT HARVARD. *Edited by William M. Wheeler and Thomas Barbour. Harvard University Press, Cambridge.* $2.50. 5¼ x 7⅞; xxxi + 202; 1933.

The Museum of Comparative Zoölogy at Harvard University possesses six Lamarck manuscripts. In this volume transcriptions of the original French texts are given together with their English translations. The first is on phrenology. Lamarck discusses Gall's theory that "our higher faculties and persistent inclinations give rise to external signs consisting in more or less conspicuous prominences of the brain case." This manuscript and the one which follows on Idea and Imagination are of considerable length. The other four, which are much briefer, are as follows: Analytical revision of human knowledge, Zoölogical questions (with drawings), Natural history, and a Report on observations made on a botanical excursion.

In an introduction the editors give a general account of the manuscripts and a comparative characterization by Crookshank of Lamarck and Darwin. As would be expected the editing is done with scholarly insight and skill throughout.

EDUCATIONAL BIOLOGY. *Second Edition. By William H. Atwood and Elwood D. Heiss. P. Blakiston's Son and Co., Philadelphia.* $2.75. 6 x 8¾; xiii + 475; 1933.

To those who are interested in the teaching of teachers of biology and who favorably received the first edition of this work, this, the second edition, will no doubt continue to be useful. In somewhat less than 500 pages, including 269 illustrations, the reader moves rapidly from centrosome to *Sequoia sempervirens*, from instinct to acquired immunity. Obviously, only the simplest and most superficial discussions can be given. Each chapter or unit is followed by a list of questions, presumably to stimulate the student to further reading, and by a short bibliography. For the most part the references are general textbooks, many of which are repeated in successive lists, and it may be doubted

that such entries as "Bulletins of the various states' Departments of Agriculture" and "Wright, *Frogs*, U. S. Bureau of Fisheries" will arouse the naive student to independent reading or introduce him to acceptable bibliographic notation.

OLD AGE DEFERRED. *The Prevention of the Disabilities and Diseases of Old Age.*

By Bernard Hollander. Watts and Co., London. 3s. 6d. net. $4\frac{3}{4}$ x $7\frac{1}{4}$; ix + 102; 1933.

This little book written by an English physician who aims to reassure those who see old age on the horizon, contains much sound information and wise advice. It begins with the question "What is old age?" and proceeds through such topics as the physical signs of senility and the mental changes which occur, the average duration of life, the chemistry of life, the chemistry of the body and preservation of virility, to general rules for a comfortable attainment of advanced years. In the section on "One of nature's remedies for premature senility" the author discusses a phase of the subject which has received far more attention in Europe than in the United States, namely, the rejuvenating powers of the waters of natural springs. The work concludes with a short list of references and a detailed index.

MEDICAL BIOLOGY. *A Laboratory Manual of Bacteriology, Mycology, Immunology, and Parasitology; Consisting of Experimental Guide, Interpretive Text, Atlas and Protocol Form.*

By William B. Sharp. University of Texas, Galveston (William B. Sharp). $4.50. $6\frac{1}{8}$ x 9; iv + 443; 1933 (paper).

A laboratory handbook of bacteriology, mycology, immunology and parasitology. It is designed to aid the student in the organization, interpretation and systematic recording of data he gathers in the laboratory. The seven parts of the manual are as follows: General bacteriology, sanitary bacteriology, milk and meat product sanitation, contamination of foods and drinking water, clinical bacteriology and medical zoölogy. Each part is divided into sections which give general discussions of the main points in a particular field, illustrations and important exercises with space for notes and records which the student may wish to record. Altogether the work contains over 100 figures. It is indexed.

THE GREAT ENIGMA. *A New View on the Outlook of Life.*

By Hugo H. Schauinsland. Translated from the German by Walter H. Schauinsland. E. P. Dutton and Co., New York. $1.25. $5\frac{1}{4}$ x $7\frac{1}{2}$; 93; 1933.

The enigma of life is how to account for the development of complete organisms, and while Dr. Schauinsland is gracious enough to concede that science has made some slight progress in describing the changes that go on in living matter he is quite firm in saying that scientific methods can never account for correlation and coordination of the parts of an organism. For this one must invoke spiritual forces; vitalism will not do because it is not potent enough. It takes real, old-fashioned, religion to explain biology. Schauinsland is so sure he is right that it is not necessary for him to argue his points, he merely tells you what is right and what is wrong. This method has one merit, certainly: it wastes little paper.

A TEXTBOOK OF GENERAL BIOLOGY.

By E. Grace White. The C. V. Mosby Co., St. Louis. $3.00. $5\frac{1}{2}$ x $8\frac{1}{2}$; 615; 1933.

An attempt has been made to write a sort of minor treatise on biology constructed on formal lines, which would give "the beginner a glimpse into all phases of biology," and so conscientiously has this plan been followed that almost every biological theory, even the newer and still dubious ones, is referred to somewhere. The treatment is uneven, as a result, and a good many parts suffer from lack of clarity of expression. There is a long glossary in the back of the book, in which numerous terms are badly defined, and a good index.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 407. Rotationsdispersion.*

By Marie Wreschner. Urban und Schwarzenberg, Berlin. 4.50 marks. 7 x 10; 92; 1933 (paper).

A brief discussion is provided of the theory and methods of polarimetric measurement with monochromatic light in the visible spectrum and also in the infra-red and ultra-violet.

HUMAN BIOLOGY

LINCOLN. *A Psycho-Biography.*

By L. Pierce Clark. Charles Scribner's Sons, New York. $3.50. 6 x 9; xv + 570; 1933.

LINCOLN AND THE DOCTORS. *A Medical Narrative of the Life of Abraham Lincoln.*

By Milton H. Shutes. The Pioneer Press, New York. $5.00. 5½ x 9; 152; 1933.

These two volumes are welcome additions to the mass of Lincolniana, particularly to the human biologist. Lincoln is one of the great type specimens of *Homo sapiens*, worthy always of more penetrating study. Somewhat belatedly it has now come to be generally accepted that in order to get any real understanding of a man's life it is necessary to know everything possible about his physical and mental well-being (or alternately ill-being). These books before us are definite and significant contributions to such knowledge about Abraham Lincoln.

Clark's treatise is, by a great deal, the more important. A careful reading of it has convinced us that it gives for the first time a really sound, trustworthy and comprehensive picture of the personality of the man. It is not news that Lincoln was a psychoneurotic. But we have not hitherto had such a clear and cogent analysis of just how and why he was such. It is obviously impossible to summarize in a paragraph of a review 570 pages of close reasoning about a complex personality. But some idea, at least, of the author's conclusions may be got from the following:

> We therefore see in the Lincoln character two violently opposing forces, intellectual and emotional. The one embracing his keen interest, his logical process of thought, his enduring grasp upon reality and his sane judgment, through which he would become a free thinker in the best sense of the term, but on the other hand we find as deeply implanted the maternal identification, the deepest emotional need of continued protective support against a loveless existence. Thus the helplessness and its needfulness are born out of the identification with the mother-image, an emotional fixation in which the need of love is overwhelming. In Lincoln we have his identification with the father by which he takes over the father's masculine strength; he places it, however, to the father-surrogate's undoing in the field of religious thought, but a still deeper implant of dependency will not let him off, for the longing for security and support from the all-giving mother is also present. No wonder the various contemporaries who happen to view but a facet, one side of Lincoln's mind formations, interpret so differently his religious life. Lincoln personifies the travail of all who would give up the longing to return to the mother's loving arms, to re-experience the Nirvana of the prenatal existence. It is indeed a Sisyphus' task for the life forces to strive to overpower the death impulses, yet for life's span Lincoln valiantly strives to ward off the death impulses, and never does he succumb completely to religious domination. He takes as his mentor the totality of the ingredients of the mind, the conscience, as his omnipresent Thou shalt and Thou shalt not.

Unfortunately Dr. Clark writes like a psychiatrist. Why it is that the modern psychiatrist, with few exceptions, feels compelled in his writing to be at once so tediously verbose and so tortuously precious, has never been made clear. To say of the evening gatherings of lawyers and judges in a dingy hotel room for a shot of whiskey before going to bed after a busy day on the circuit in the middle west nearly a century ago that "in their recalescent glow one catches a strange illumination that this conviviality borders closely upon a sensuous ecstasy, a dionysiac orgy that seduces men from their homes" (p. 132) is not the sort of writing likely to win sensible readers.

Dr. Shutes' book is smaller and more matter of fact. It furthermore is not written in the irritating historical present tense. It confines itself to an account of practically all the contacts of Lincoln and his family with the medical profession, going into such details as his drug store bills, the prescription for his spectacles, etc. It forms an excellent supplement and foil to Pierce's more expansive treatise.

Both books have bibliographies and indices. Both are well worth reading.

ON ANCIENT CENTRAL-ASIAN TRACKS.
Brief Narrative of Three Expeditions in Innermost Asia and North-Western China.
By Sir Aurel Stein. The Macmillan Co., New York. $10.00. 6½ x 9¼; xxiv + 342; 1933.

In this book, based on a course of Lowell lectures, the distinguished author presents a succinct account of his explorations, archeological and geographical, in Chinese Turkestan and the neighboring regions. After two introductory chapters, dealing with the geography and history of central Asia, a narrative of his travels and excavations on his three expeditions of 1900 to 1901, 1906 to 1908, and 1913 to 1916, is given. Among his interesting finds in the ruined cities of the desert were frescoes and votive panels of painted wood from Buddhist shrines in a style derived from the Graeco-Buddhist art of north-west India; a panel representing Rustam, the great hero of Persian epic legend, as a Buddhist divinity; documents on wood in Kharoshthi, an ancient Indian script; and clay seals bearing the figures of Pallas Athene, Eros and Heracles. He was also able to trace the remains of the wall which the Chinese Emperors of the Han dynasty in the second century B.C. built to protect the corridor between China and the west against Hunnish raids. His discoveries thus illustrate the singular mixture of Indian, Greek and Chinese influence to which this far off region of central Asia was subjected. The most interesting of his finds, however, was a great mass of Buddhist and secular manuscripts and painted banners which had been hidden for nearly a thousand years in a rock-cut chamber of the Caves of the Thousand Buddhas. Among the discoveries here were a block printed roll dated A.D. 868, the oldest printed book yet found; Manichaean texts which throw new light on that hitherto little known religion; and the "most remarkable, comprehensive and also best preserved" manuscript of the earliest Turkish literature.

This is a fascinating book, made still more vivid by excellent illustrations, many of them in color. It contains also a map of Chinese Turkestan and the adjacent regions, an index and a bibliography of Sir Aurel Stein's writings.

ADVENTURES OF IDEAS.
By Alfred N. Whitehead. The Macmillan Co., New York. $3.50. 5¾ x 8½; xii + 392; 1933.

The title of this book, Professor Whitehead explains, bears two meanings. On the one hand, the book traces the adventures of certain ideas in promoting the slow drift of mankind towards civilization; on the other hand, the book itself is the fruit of the author's adventure in framing a speculative scheme of ideas which shall be explanatory of the historical adventure.

The first adventure is in the social realm: that of Plato's idea of the essential greatness of the human soul in its effect on slavery. The classical civilization was based on slavery; Plato himself must have been a slave owner. Yet his concept working on the minds of the Stoic lawyers of the Roman Empire, of the Christians, of the sceptical humanitarians of the eighteenth century, produced first the amelioration and finally the abolition of slavery.

Part II, dealing with the influence of scientific ideas upon European culture, ends rather curiously with an appeal to the Protestant clergy for leadership in the new Reformation which is in progress. Just what the religion issuing from this new Reformation will consist of is not entirely clear to us, but there seem to be three main ingredients: (1) the Platonic doctrine that the divine element in the world is a persuasive, not a coercive element; (2) Jesus as the supreme illustration of this doctrine; (3) the doctrine of the early Christian theologians of the immanence of God in the world.

Part III deals with the more particular problems and debates of the philosophers; while Part IV treats of the five qualities that define a civilized society: Truth, Beauty, Adventure, Art, Peace. The latter refers, not to political relations, but to "a quality of mind steady in its reliance that fine action is treasured in the nature of things."

Evidently Whitehead has traveled a long distance from the *Principia Mathematica*. Yet it is perhaps significant that Russell has journeyed along much the same road. After all, man is not a disembodied intellect but a social animal, an agent faced with the necessity for making decisions

between alternative actions, and longing to find some ultimate goal towards which his actions may tend. "Life" said Samuel Butler, "is the art of drawing sufficient conclusions from insufficient premises." And if the conclusions are not always wholly sufficient, it is of the essence of adventure that it does not always reach the sought for goal.

OLD AGE AMONG THE ANCIENT GREEKS. *The Greek Portrayal of Old Age in Literature, Art, and Inscriptions, with a Study of the Duration of Life Among the Ancient Greeks on the Basis of Inscriptional Evidence.*

By Bessie E. Richardson. The Johns Hopkins Press, Baltimore. $4.00. 6 x 9; xv + 376; 1933.

This useful addition to the literature of human biology presents the results of a thorough and painstaking combing of the classics for everything that could be found relating to longevity, senescence and senility among the Greeks. The material so collected is then discussed from a variety of angles. Seven of the thirteen chapters (I, VI, VII-XI inclusive) deal with the physical aspects of senility, either as revealed by written descriptions and allusions, or by vase paintings, or by one or another form of sculpture. Of the remaining chapters II concerns itself with the mental and emotional characteristics of senility; III with the duties and interests of the aged citizen; IV with the attitude of the Greeks towards the aged; V with rejuvenation. Chapter XII lists remarkable examples of longevity, and XIII attempts, on the basis of the stated ages at death in the sepulchral inscriptions of 2022 persons, to determine the distribution of duration of life. The average age at death turns out to be 29.43 years. But there is a patent deficiency of records for deaths under 20 years. Altogether it is to be regretted that the author did not seek the advice and guidance of a competent biostatistician when preparing this chapter. She plainly lacks a clear understanding of the various technical concepts and procedures of either the statistical or the actuarial calculus.

An indication of the thoroughness of the work on the literary side is given by the first entry in the selected bibliography, which reads as follows: "A. Literature. Nearly all the Greek authors have been consulted." The documentation (in footnotes) throughout is meticulous. The illustrations are numerous and excellently reproduced. Besides a general index there is a concordance to literary passages, and a concordance and index to art, tabulating each art object used in the study.

No library or laboratory dealing with human biology can afford to be without this book.

ARCTIC VILLAGE.

By Robert Marshall. Harrison Smith and Robert Haas. $3.00. 5¾ x 8½; xii + 399; 1933.

Here is an entertaining book of much interest and value to students of human biology in the broadest sense of the term. The author, a trained botanist and forester, first spent a summer in the village of Wiseman in the upper reaches of the Koyakuk River, well above the Arctic Circle in Alaska, and liked the place and its inhabitants so much that he went back again and stayed more than a year. The book is a penetrating description and analysis of the inhabitants as individuals and as a social group, in their relations to each other and to their environment, an environment extremely harsh and forbidding by conventional standards and attitudes.

The net upshot of the study is to demonstrate that the people of Wiseman are just as well off in terms of human happiness as people anywhere else in the world, and in some respects better off. This result will strike the average city dweller as more remarkable than it really is. To anyone who has had the good fortune to have been born and brought up in, or to have lived any considerable length of time in a remote backwoods community, some of Marshall's findings in Wiseman will seem commonplace, so much so in fact as to throw parts of the book almost into James's category of the "painstaking delineation of the obvious."

The total population of Wiseman consisted of 127 persons, of whom 77 were whites, 44 Eskimos, and 6 Indians. The

author's technique was to become intimately acquainted with these persons as individuals, test and measure them in a variety of ways, psychologically and physically, and at the same time by becoming himself wholeheartedly a constituent member of the community get a thorough understanding of the organization and interplay of social forces and relations. That Dr. Marshall is sympathetic to the sort of life he found is sufficiently indicated by the dedication of the book, in which he calls it "the happiest civilization of which I have knowledge."

The book is a contribution to human biology of real significance and importance. Its thirty-seven chapters are ordered in seven parts, dealing respectively with the background, the people, the economic life, the communal life, the sexual life, the recreational life, and Koyakuk philosophy. The illustrations are abundant and beautifully reproduced from the author's own photographs. There is an excellent analytical index.

SOME BASIC STATISTICS IN SOCIAL WORK. *Derived from Data of Family Agencies in the City of New York.*

By Philip Klein with the Collaboration of Ruth Voris. Columbia University Press, New York. $3.50. 5½ x 8½; xiv + 218; 1933.

This study dealing with family welfare work in Manhattan and the Bronx in the City of New York was commenced before the depression era and covers two years of the depression itself. Four agencies coöperated in the work: The Association for Improving the Condition of the Poor, the Catholic Charities, the Charity Organization Society, and the Jewish Social Service Association. The investigators "attempt to formulate, for one of the most important social work activities, statistics appropriate to its task, accurate and uniform, and capable of being related to community life." The specific objectives of the inquiry growing out of this general purpose are defined in the form of a series of questions. Then follows a discussion of the relation between economic conditions and the operations of the family agencies, the nature and inclusiveness of the organizations studied, the merits of statistical units employed in measuring their work, the possibility of obtaining accurate and uniform statistics and of distributing them by small areas, and finally the applicability of the findings of the study beyond the immediate field of family social work or the particular territory covered by our agencies.

The work includes numerous tables, graphs, and figures. In four appendices will be found notes on collecting data and on additional statistical material. There is an index. Porter R. Lee contributes a foreword.

HOLLOW FOLK.

By Mandel Sherman and Thomas R. Henry. Thomas Y. Crowell Co., New York. $2.00. 5⅛ x 7½; viii + 215; 1933.

The early migrations of settlers into West Virginia and Ohio in Colonial times left small groups of people of English and Scotch-Irish ancestry stranded in the hollows and valleys of the Blue Ridge Mountains of Virginia. Their descendants are there still; if their parents happened to have settled in the lower valleys they have been involved to varying degree in the social and economic changes of the nation, but in the more inaccessible hollows are little communities of highly inbred people who have been almost completely isolated from the rest of the world for generations and who have forgotten what schools, churches, and systems of government are.

The material which forms the basis of this story of mountain people was obtained from a study made during a period of two years. Two psychologists and their assistants, a nutritionist, a psychiatrist and sociologists took part in the investigation. In addition, a field worker intimately acquainted with the mountain people lived amongst them continuously during the two years gathering social and economic data. Not only did these workers make frequent trips to the mountains to administer tests, but they also lived for varying periods in the cabins of the mountain people in order to become familiar with their habits, customs, daily routine, desires and thoughts. The names of the communities and inhabitants are fictitious.

A journalist and a psychiatrist collaborated in writing this book, and they have an interesting story to tell.

FIGHTING THE INSECTS. *The Story of an Entomologist. Telling of the Life and Experiences of the Writer.*

By L. O. Howard. The Macmillan Co., New York. $2.50. 5¾ x 8½; xvii + 333; 1933.

This charming autobiography by the *doyen* of American entomologists embodies a great deal of general biological, social, and governmental history, as well as strictly entomological. Dr. Howard's manifold talents and graces combined with his long-held official position as chief entomologist of the federal government make his life an unusually interesting and varied one. He can look back over it, as he does in this book, with the satisfaction of having missed but few pleasant bets, as the phrase goes. While he is very modest about it all, his solid achievements must also be a great comfort to his declining years, for it can be quite truly and literally said of him that in his life time he changed the status of economic entomology, and brought it to a position of dignity and importance second only to medicine among the applied biological sciences.

This story of his life is most entertainingly written, chatty and digressive as an autobiography ought to be. Dr. Howard has long had a great reputation as a *raconteur*, and happily he puts into this book many of his best stories, some of them familiar to the older generation of biologists to be sure, but very much worthy of permanent record for the delectation of generations to come.

Altogether we congratulate the genial and urbane author, with deep sincerity and hearty good wishes, upon a good life pleasantly and usefully lived, and upon his delightful account of it. May God bless and preserve him for many years yet.

WILLIAM BARTRAM. *Interpreter of the American Landscape.*

By N. Bryllion Fagin. The Johns Hopkins Press, Baltimore. $2.25. 6 x 9; ix + 229; 1933.

In the history of American natural science the name of Bartram holds an honorable place. John Bartram was a Pennsylvania farmer who established the first important botanical garden in America, helped Franklin to found the American Philosophical Society, and was regarded by Linnaeus as "the greatest natural botanist in the world." His son William spent five years in botanical explorations in the Southern colonies, which were described in his *Travels through North and South Carolina, Georgia, East and West Florida, the Cherokee Country, the Extensive Territories of the Muscogulges, or Creek Confederacy, and the Country of the Chactaws; containing an Account of the Soil and Natural Productions of those Regions, together with Observations on the Manners of the Indians.* (Philadelphia, 1791). The book was soon reprinted in England and Ireland, was translated into German, Dutch and French, and was among the chief sources from which Coleridge, Wordsworth, Chateaubriand and other writers of the Romantic school drew their ideas of the subtropical landscape and of the noble savage. In it we find the various sides of Bartram's character represented: the careful observation of the naturalist, the esthetic appreciation of Nature of the artist, the rhapsodic piety of the Quaker. Mr. Fagin gives an account of Bartram's life, his philosophy of Nature, his studies of the American Indian, his treatment of the southern landscape, and his influence on literature. There is a bibliography of twelve pages and an index. It is to be hoped that this scholarly study will aid in making a delightful book better known.

GYPSUM CAVE, NEVADA. *Report of the Second Sessions Expedition. Southwest Museum Papers Number Eight.*

By Mark R. Harrington. Southwest Museum, Los Angeles. $2.50. 7 x 10⅜; ix + 197; 1933 (paper).

In view of the discussions that have gone on for many years concerning the inhabitation of America by very early man this investigation, demonstrating as it does that man must have been in Western United States as early as the beginning of the late paleolithic period, or around 20,000 B.C., is a most welcome contribution to the archeology of this country.

Gypsum Cave, situated in southwest Nevada, is a limestone cave of paleozoic age; it shows considerable tilting distortion and the action of heat. The cave measures 300 feet in length and divides naturally into five rooms which have been the depository for refuse and articles belonging to man and animals for many ages. Indications that the cave was inhabited by pleistocene animals were furnished most conclusively by (1) the large deposits of dung identified as belonging to the ground sloths of that period, (2) the discovery of the skull of the giant sloth *Nothrotherium shastense*, and (3) bones belonging to pleistocene species of the camel and horse. Associated with these findings are many obviously human artifacts, the most common of which were darts, painted dart-shafts, dart points, and flint articles. Although no actual skeletal remains of early man were unearthed, there can be no doubt that man inhabited the cave and met face to face animals long since extinct and definitely living in this country during the paleolithic era.

This is a contribution of first-rate importance.

DISPLACEMENT OF MEN BY MACHINES. *Effects of Technological Change in Commercial Printing.*

By Elizabeth F. Baker. Columbia University Press, New York. $3.50. 6 x 9; xxii + 284; 1933.

The aim of this investigation was to determine the extent to which men have been displaced by machines in the printing industry, which has been mechanized to a high degree, particularly within the last 20 years, and in which competition is unusually keen. Remarkably enough, "despite these improvements in machinery, the number of workers employed in book and job printing, instead of decreasing has steadily grown. This appears to be explained by the relatively low man-displacing power of the new machines, accompanied by an important increase in the consumption of printing." It is the unskilled assistants who are finding reëmployment increasingly difficult (there is normally a very high labor turn-over in this trade) and the human problem involved in the efforts of these men to retain their place in the industry takes up a good deal of the book. Several kinds of study are represented, and it becomes an important contribution because it appears to be one of the first attempts at a really thorough study of the labor conditions prevailing within a whole industry. It is beautifully printed and is provided with a good index.

THE STORY OF KALAKA. *Texts, History, Legends, and Miniature Paintings of the Śvetāmbara Jain Hagiographical Work. The Kālakācāryakathā. Smithsonian Institution, Freer Gallery of Art, Oriental Studies, No. 1.*

By W. Norman Brown. Smithsonian Institution, Washington. $2.00 (paper); $2.50 (cloth). 10⅓ x 14; viii + 149 + 15 plates; 1933.

Although the Jains have never been one of the more numerous of Indian sects the importance of their religious art and literature is out of proportion to their numbers. In this book Professor Brown has edited the various versions of the legend of the Jain saint Kalāka, or rather of several saints of the name who have been more or less confused with one another. In one episode of the legend, the wicked king Gardabhilla abducts the nun Sarasvatī for his harem. Kalāka thereupon conspires with the Scythians, who invade the country and make themselves rulers of it. This adventure of Kalāka in politics seems scarcely consonant with the Jain principle of doing harm to no living creature. Apparently in India as in some other countries when the principles of a religion conflict with the welfare of the church it is just too bad for the principles.

The book contains beautiful reproductions, several in color, of the miniature paintings which illustrate the manuscripts. These belong to the little known Western Indian school which preceded the Rajput and Mughal styles.

HISTORY AS A SCIENCE.

By Hugh Taylor. Methuen and Co., London. 7s. 6d. net. 5½ x 8¾; vii + 138; 1933.

Mr. Taylor's thesis is that the development of history as a science has been retarded by the circumstance that historians in general have approached their subject from the viewpoint of the moralist rather than from that of the scientist, that they have started with a prepossession in favor of freedom, or constitutionalism, or what not, and have interpreted the data to conform to their prepossession instead of deducing generalizations from an unbiassed study of the facts. However, it is easier for a writer to advocate "a passionless attitude restricted to the sole purpose of gaining knowledge" than for him to adopt it in actual practice. There is the complication that the student of human relations is himself a man and with the best will in the world to be objective finds it difficult to study them with the same detachment with which he might observe the relations of different castes of bees. In Mr. Taylor's own application of his theories to the historical phenomena of government, war and revolution we suspect from his somewhat emotional tone that his conclusions are really as much presuppositions as those of the historians whom he criticises.

THE ISLE OF AUKS.

By Nicholas Polunin. Edward Arnold and Co., London. 10s. 6d. net. 5½ x 8½; 253; 1932.

This is a narrative of the Oxford University Expedition of 1931 up the coast of Labrador to Akpatok, an unexplored island in Hudson Strait. Many geographical and geological data were obtained, as well as information on plants and birds, polar bears and Eskimos. The latter are coming to rely more and more on the Hudson's Bay Company for sugar, flour, tea, pork and tobacco, for which they exchange their fox and seal skins. They have many stories of the Tunnits, the extinct race of giants who lived by stealing from the Eskimo hunters, until they were killed off by the Eskimo women, who used to creep up while they were asleep and drill holes in their foreheads.

Akpatok proved as forbidding as the Eskimos had reported it to be, a barren tundra bounded by almost inaccessible cliffs, swathed in fog or beaten by tempest. However, the party succeeded in establishing a camp and exploring the island, but the expedition ended in tragedy when "Polly" and "Kit" lost their way on a collecting trip and the latter died of exposure. The narrative of this trip is as graphic an account of the difficulties of Arctic travel as one might wish to find.

GOD'S CANDLELIGHTS. *An Educational Venture in Northern Rhodesia.*

By Mabel Shaw. Edinburgh House Press, London. 2s. 6d. net. 5⅜ x 8; 197; 1932.

This book is based upon letters written by the authoress during a period of seventeen years in the mission school for girls which she founded under the auspices of the London Missionary Society, at Mbereshi in Northern Rhodesia, Africa. It tells

> of an attempt to conserve all that is true and good in the old life and build upon it; to link the past on to this new and baffling, and, to the Bantu, exciting present; to carry over from the old life that steadying, unifying belief in the continuity of life, its uninterrupted flow and rhythm; and so to present the Christian faith to the community and to the individual that they see it not as the white man's religion, something likely to be as useful to them as his money is, but as the fulfilment of that towards which their fathers groped; a way of life, not through foreign lands, but through the familiar ways of their own thought and belief.

The book is of value not only to those engaged in missionary work, but also to everyone interested in the education of primitive peoples. If all missionaries were like Miss Shaw their profession would be more highly respected than it is.

SOCIAL PATHOLOGY.

By John L. Gillin. The Century Co., New York. $3.75. 5⅞ x 8¾; ix + 612; 1933.

Social Pathology is here defined as "the study of man's failure to adjust himself and his institutions to the necessities of existence to the end that he may survive and meet fairly well the felt needs of his nature." The author believes that social pathology should be interpreted in terms

of existing sociological theories. The book is divided into five parts. Part I deals with the *Pathology of the Individual*, wherein the author discusses mental and physical ailments. Part II is a discussion of the *Pathology of Domestic Relationships*. Part III, *The Pathology of Social Organization* is a discussion of urban and rural disorganization and class and group disorganization resulting from the rapid industrialization and consequent growth of large cities. Part IV, *The Breakdown of Economic Relations*, discusses the maladjustments arising from our present economic situation. Part V, *The Pathology of Cultural Relations*, is devoted to a discussion of the changes taking place in our religious, moral, and ethical mores.

This should make an excellent textbook.

ATA KIWAN. *Unbekannte Bergvölker im tropischen Holland.*

By Ernst Vatter. Bibliographisches Institut AG, Leipzig. 18 marks. 6½ x 9½; iv + 294; 1932.

Ata Kiwan, meaning "People of the Mountains," is the name by which the natives of the mountainous Solor-Alor Archipelago call themselves. This group of islands lies just east of Java and Bali and consists of Flores, Salor, Adonare, Lomblem, Pantar and Alor. The author of this book and his wife spent eight months on the archipelago and this account of their travels, the geography of the islands, the physique of the peoples, their culture, customs and ceremonies makes interesting reading. It is noteworthy as a record of a culture which is fast being superseded by European civilization. The natives differ from island to island not only in customs but also in physique and temperament, those of East Flores being very friendly and gentle, while those of Adonare will commit murder upon the slightest provocation. An index and a bibliography are provided.

ORIGINS OF SACRIFICE. *A Study in Comparative Religion.*

By E. O. James. John Murray, London. 10s. 6d. net. 5½ x 8⅝; xvi + 314; 1933.

In this book Dr. James traces the evolution of sacrifice from its beginnings to its place in the religions of civilization. The central conception underlying the institution is, he concludes, the giving of life to promote and conserve life, to augment the power of the god and enable him to carry out his functions, to strengthen the worshipper against evil, or to set up a bond of union with the supernatural powers. With the spiritualization of the concept of Deity the primitive idea of sacrifice as a necessary condition for the continued existence of the gods has given place to the idea of free-will offerings of gratitude or of acts of atonement for wrong-doing. The evolution of sacrifice in Judaism, Christianity and the religions of the far East is traced in detail. There is a bibliography of 19 pages and an index.

THE GERMAN JEW. *His Share in Modern Culture.*

By Abraham Myerson and Isaac Goldberg. Alfred A. Knopf, New York. $1.25. 5 x 7⅜; xxii + 161; 1933.

Dr. Myerson is professor of neurology at Tufts College Medical School and Dr. Goldberg lecturer on Hispano-American Literature at Harvard. Their book aims to present a brief summary, obviously as anti-Nazi propaganda, of what the German Jew has done in the past and is doing in the present in medicine, physics, chemistry, philosophy, mathematics, music, art, literature, journalism, drama, stage and cinema. After a short history of anti-semitism in Europe the authors give an imposing list of German Jews, with comments on their lives and contributions in these various fields. The index of names covers 9 pages.

THE HAND OF DESTINY. *The Folk-Lore and Superstitions of Everyday Life.*

By C. J. S. Thompson. Rider and Co., London. 12s. 6d. net. 5½ x 8½; 303; 1933.

In this book about 1,500 superstitions are classified under twenty-five chapter headings such as birth, childhood, courtship, marriage, the evil eye, the hand, face, apparel, food, healing, family curses, death, bones, sailors, animals, plants,

amulets, numbers, drinking and games. The superstitions are merely described without any attempt at explanation or generalization. However, it is evident from many of them that our forefathers had a vivid, if somewhat uncritical, interest in somatology. There is an index.

THE BIOLOGICAL CONCEPT OF MAN. *A Brief Introduction.*

By A. H. Miller. A. H. Miller, Branksea Tower, Parkstone, Dorset. 2s. 6d. 5½ x 8¾; 35; 1933 (paper).

When a successful and undoubtedly busy practitioner of medicine undertakes, in 35 pages, to write a biological concept of man, it is not unreasonable to expect the work of a genius. Such good fortune is, however, not apparent in Dr. Miller's paper. As nearly as can be ascertained, the author's idea is that present day medical diagnosis, therapeutics, and medical economics can and should be revolutionized by the simple but mysterious procedure of "rejecting altogether speech as an aid to diagnosis." Reginald the Office Boy raises the question as to whether this means that in nose and throat practice the patient is not to say "Ah."

RASSENKUNDE UND RASSENGESCHICHTE DER MENSCHHEIT. *Dritte Lieferung (Bogen 19–27). Vierte Lieferung (Bogen 28–36).*

By Egon F. von Eickstedt. Ferdinand Enke, Stuttgart. 10 marks each. 7⅛ x 10⅝; 144 each; 1933 (paper).

The first two numbers of this excellent series of anthropological and biodynamic studies of the peoples of the world were noticed in the last number of this REVIEW. The present numbers contain the conclusion of the treatment of the inhabitants of Asia (begun in *Lieferung* 2), the peoples of Europe and Africa north of the Sahara, and the negro population of Africa.

THE COCOPA. *University of California Publications in American Archaeology and Ethnology, Volume 31, No. 5.*

By E. W. Gifford. University of California Press, Berkeley, $1.00. 6¾ x 10¼; 78; 1933 (paper).

These tribes are of the Yuman family and inhabit the regions around the head of the Gulf of California. The volume is only part of a basic survey of the Yuman group, and as such consists chiefly of notes on the culture, no attempt being made at a pleasant or readable style. The author concludes that the Cocopa culture is very similar to the two great Colorado River tribes, Mohave and Yuma.

THE LAW AGAINST ABORTION. *Its Perniciousness Demonstrated and Its Repeal Demanded.*

By William J. Robinson. Eugenics Publishing Co., New York. $2.15. 5⅜ x 8½; 123; 1933.

Here are 123 pages of chatty propaganda with "case histories" written in the Robinsonian style for the physician and the layman.

ZOÖLOGY

THE HAPPY BEAST *in French Thought of the Seventeenth Century.*

By George Boas. Johns Hopkins Press, Baltimore. $2.00. 5½ x 8; vii + 159; 1933.

Mankind may be divided into those who admire civilization and those who do not. The former regard the process of social evolution as leading upwards; the latter look back to their pre-civilized fellows as closer to nature and therefore more virtuous than civilized man. Carrying this viewpoint one step farther some of them, for whose doctrine Professor Boas coins the word "Theriophily," find the true models of virtue and happiness in the animals. This attitude dates back to Plutarch at least, but its advocacy by Montaigne and his disciples made it a subject of considerable controversy in seventeenth century France. In reply to the objection that man's possession of reason makes him superior to the beasts some theriophiles maintained that reason is a curse not a blessing, some that the beasts also possess reason, while others seized both horns of the dilemma. But any equation of man with the other animals was felt by many to be dangerous in its moral effect. Various reverend Fathers began to beat the

drums, while Descartes set forth his famous doctrine that the beasts are merely machines. Professor Boas traces the various stages of the controversy until in the eighteenth century it was transferred from the field of theology to that of biology.

LES PHÉNOMÈNES SOCIAUX CHEZ LES ANIMAUX.

By François Picard. Armand Colin, Paris. 10.50 francs. 4½ x 6⅞; 201; 1933 (paper).

Zoölogists, biologists, and sociologists interested in the study of the biology of social organisms will find much that is of value in this little brochure. The author discusses very thoroughly the social phenomena of living organisms from the lowest forms to man. He finds that sociability and society are based everywhere in the last analysis upon an instinct of reciprocal attraction or inter-attraction. He classifies these phenomena into definite types, distinguishing carefully between crowds and mere aggregations, and the truly social groups, associations, societies and biocenoses. In his final chapter dealing with human society, he takes special issue with the theory of Durkheim and his school, according to which society is regarded as having an artificial, antibiological origin, being based on arbitrary constraint, and likewise with the thesis of Fustel de Coulanges and others who derive society from the family. There is a short bibliography and a table of contents.

THE JUNGLE BEES AND WASPS OF BARRO COLORADO ISLAND. *(With Notes on Other Insects.)*

By Phil Rau. Phil Rau, Kirkwood, Mo. $2.75. 6 x 9⅛; 324; 1933.

Much new and valuable material concerning the jungle bees and wasps of Barro Colorado Island is to be found in this book. The author writes entertainingly concerning the ecology and biology of these insects and their behavior attributes and adaptations. There is a section on the behavior of the giant carpenter bee, which, although not found in Barro Colorado, is of tropical origin. In the final section on mind as a forerunner of evolution the author compares the efficiency of evolution by natural selection of variations alone, and by natural selection plus mental and nervous direction. In an appendix are given descriptions of three new species of Polybia wasps by Dr. Joseph Bequaert. The volume is interestingly illustrated and contains an index. The book is an important contribution to the literature of general biology as well as entomology.

BRIEF BIRD BIOGRAPHIES. *A Guide to Birds Through Habitat Associations.*

By J. Fletcher Street. Grosset and Dunlap, New York. $1.00. 7½ x 10; 160; 1933.

The purpose of this volume is to render bird identification easy to the average individual. The birds listed are those which are commonly found east of the Mississippi valley, excluding the Southern States. One hundred and fifty species are illustrated and their outstanding traits and habits briefly described. There are textual references to 64 others. The author has adopted the unusual but practically useful method of grouping the birds according to their habitat associations. The drawings are in black and white, each species being exhibited as it appears in its customary haunts. It is believed that by this method it is possible to fix a bird more definitely in one's mind than by emphasizing (often unsatisfactorily) plumage coloring.

FISHES AND FISHING IN LOUISIANA. *Including Recipes for the Preparation of Seafoods. State of Louisiana, Department of Conservation, Bulletin No. 23.*

By James N. Gowanloch. Department of Conservation, New Orleans. Free; if mailed, 50¢ to cover postage. 6 x 9; 638 + folding map; 1933 (paper).

In this volume an earlier work (previously mentioned in these pages) has been revised and enlarged. It includes both the salt and fresh water fishes of Louisiana,

together with a description of the appropriate method of capturing them, typical Southern ways of cooking them, and the laws of the State which govern the activities of both the angler and the commercial fisherman as concerns the Division of Fisheries.

The book is generously illustrated and well indexed. Two maps provide the reader with charts of the fishing grounds.

LES ARACHNIDES (*Scorpions, Araignées, etc.*). *Biologique Systematique. Encyclopédie Entomologique, XVI.*

By Lucien Berland. Paul Lechevalier et Fils, Paris. 150 francs (paper); 160 francs (cloth). 6½ x 10; 485; 1932.

Although the morphology, biology, classification, and geographical distribution of all the arachnids are treated in this book, the greater part is devoted to the spiders. It is well illustrated with drawings and maps and equipped with indices—author, names of species, as well as an index of biological and anatomical terms. The bibliographies given at the ends of the chapters total over 400 titles. A useful handbook for the naturalist.

LOS VERTEBRADOS EXHIBIDOS EN LOS ZOOLÓGICOS DEL PLATA. *Memorias del Jardin Zoológico de la Plata, Rep. Argentine (1930–1931), Tome IV.*

By Carlos A. Marelli. Ministerio de Obras Públicas de la Provincia de Buenos Aires, La Plata. 7¼ x 10¾; 275 + 84 plates; 1931 (paper).

A list of mammals, birds and reptiles in the Zoological Gardens at La Plata, Argentina. Their Latin and common (Spanish) names, native habitat, and references to pictures, are given. The book is equipped with indices of Latin and Castilian names, and numerous plates, a few of which are in colors.

LEHRBUCH DER ENTOMOLOGIE.

By Hermann Weber. Gustav Fischer, Jena. 36 marks (paper); 38 marks (cloth). 6⅝ x 9⅞; xii + 726; 1933.

An excellent reference and textbook with very good illustrations. The first six chapters are respectively devoted to a discussion of (1) the skeletal and muscular systems, (2) the nervous system and sense organs, (3) integration of the sense organs, (4) digestion and assimilation, (5) reproduction and development, and (6) ecology. The seventh chapter gives a detailed classification.

INVERTEBRATE ZOÖLOGY.

By Robert W. Hegner. The Macmillan Co., New York. $3.75. 5⅝ x 8½; xiii + 570; 1933.

About 400 illustrations appear in this excellent textbook designed for the second course in college zoölogy, in addition to eight plates showing the anatomy of animals to be dissected in the laboratory. In style it is very much like Hegner's widely used *College Zoology*. The text is concisely written, and is provided with short, selected bibliographies at the end of each chapter, and with a good index.

THE JACKAL (*With Notes on Other Quarry*).

By George Hurst. The Masters of Foxhounds Association of India, C. R. E.'s Office, Peshawar, N.-W.F.P. Rs. 3/7. 5⅜ x 8¾; iv + 46; 1932–3 (paper).

This little book, written primarily for the sportsman in India, deals mainly with the jackal, which is a far more satisfactory quarry than the fox in that country. Many interesting notes on jackal habits are reported which the naturalist will not find elsewhere on record. In the text are a number of diagrams, illustrating methods of baiting and the huntsman's *cast*. There is no index.

LA VIE DES CRAPAUDS.

By Jean Rostand. Librairie Stock, Paris. 12 francs. 4½ x 7½; 224; 1933 (paper).

A highly readable story of the life of the common toad, *Bufo vulgaris*, beautifully written for the layman interested in natural science. This brochure belongs to the series *Les Livres de Nature* published under the direction of Jacques Delamain.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 411. Methoden der Tierhaltung und Tierzüchtung.* Containing following articles: *Methoden zur Untersuchung von Wasserhymenopteren*, by M. Rimsky-Korsakow; *Fang und Züchtung von Strepsipteren*, by Werner Ulrich; *Sammeln und Erforschung der Bienen- und Wespennester*, by S. I. Malyshev.

Urban und Schwarzenberg, Berlin. 7.80 marks. 7 x 10; 162; 1933.

In this number of the Abderhalden *Handbuch* are given methods for the collection and study of insects. Rimsky-Korsakow deals with the aquatic Hymenoptera and their use in morphologic, physiologic and genetic studies; Ulrich with the Strepsiptera; and Malyshev with the study of the nests of bees and wasps. Each part is furnished with a bibliography.

SURPRISES.

By Edith M. Patch and Harrison E. Howe. The Macmillan Co., New York. 84 cents. $5\frac{1}{2}$ x $7\frac{1}{4}$; xiii + 307; 1933.

THROUGH THE SEASONS.

By Edith M. Patch and Harrison E. Howe. The Macmillan Co., New York. 88 cents. $5\frac{1}{2}$ x $7\frac{1}{4}$; xiv + 331; 1933.

These two books for tiny tots are written in the same manner and for the same purpose as earlier books by the first of the authors, which have already been noticed in these pages. The books are designed for primary school use.

BOTANY

THOMAS JOHNSON. *Botanist and Royalist.*

By H. Wallis Kew and H. E. Powell. Longmans, Green and Co., London. 8s. 6d. net. $5\frac{5}{8}$ x $8\frac{5}{8}$; xi + 151; 1932.

The author's task has not been an easy one. At the time Johnson lived (the early part of the seventeenth century) there were many of the same name in England, of whom five were apothecaries. Not much is known of Thomas Johnson's personal life but all authentic records of his activities have been laboriously collected and recorded. Johnson's first publications were concerning his plant hunting expeditions, "simpling voyages" into Kent and Hampstead Heath. The *Mercurius Botanicus* (1634 and 1641), an attempt to enumerate all the known British plants, was his most important work, although his fame rests chiefly on the very excellent revision that he made of Gerard's *Herball* in 1632. The amount of labor involved to complete this edition within the allotted time of one year, and the very high standard of the work done testify to Johnson's great ability. During the Civil War in England he joined the Royalist forces, where, although publicly not pretending to valor, he undertook and performed many daring exploits. He was fatally wounded in battle in 1644. The book includes a list of the works, editions etc., by Thomas Johnson, a number of illustrations, and an index.

THE FRESH-WATER ALGAE OF THE UNITED STATES.

By Gilbert M. Smith. McGraw-Hill Book Co., New York. $6.00. $5\frac{7}{8}$ x 9; xi + 716; 1933.

This book fills a real need in a very satisfactory manner.

The following pages have been written with a twofold purpose: to enable the student to identify the fresh-water algae of this country; and to summarize the morphology and life histories of these algae. All genera found in this country are described in detail, and an illustration is given for one or more species of each. The general key on page 626 has been so constructed that vegetative characters are utilized as far as possible, and reproductive characters are included only where they are essential for the recognition of a genus. In the case of genera with fewer than 10 species occurring in this country, there is a very brief characterization of the different species. No attempt is made to distinguish between species of the larger genera. Except for certain of the rarer genera, known only from one or two stations, there is no mention of geographic distribution.

There is an extensive bibliography and an excellent index.

TRAITÉ DE CYTOLOGIE VÉGÉTALE.

By A. Guilliermond, G. Mangenot and L. Plantefol. E. Le François, Paris. 250 francs. $6\frac{1}{2}$ x $9\frac{7}{8}$; vi + 1195; 1933 (paper).

Compared with American and German

works on plant cytology this treatise is less exclusively limited to nuclear morphology and the relation of cytology to genetics, and includes certain aspects of cellular metabolism. It is a valuable and authoritative contribution to the subject and it should be useful to specialists in several other fields as well. Some idea of the scale on which it was executed can be gained from the sizes of the bibliography (which covers 105 pages) and of the separate indexes for authors and subjects (which amount to 50 pages). Unfortunately, however, these contain an irritating number of errors.

B. CARYOCYANEUS BEIJERINCK-DUPAIX 1930. *Étude Morphologique et Biologique. Recherches sur le mécanisme du phénomène de Charrin et Roger. (Agglutination sérique des Bactéries).*

By Andrée Dupaix. Le François, Paris. 50 francs. 6½ x 10; xv + 350; 1933 (paper).

Mlle. Dupaix has included in this summary of the knowledge concerning the *Bacillus caryocyaneus* Beijerinck-Dupaix 1930, the results of her own experiments conducted in the laboratory of the eminent microbiologist Lasseur at Nancy. The first part of the book is devoted to the morphology and physiology of bacteria, and the physical and chemical conditions which influence the life and mutations of *B. caryocyaneus*. The second part concerns the mechanism of agglutination. Extensive bibliographies are given with each chapter. The list of "general conclusions" covers 13 pages.

THE CULTIVATED CONIFERS IN NORTH AMERICA. *Comprising the Pine Family and the Taxads.*

By L. H. Bailey. The Macmillan Co., New York. $7.50. 7 x 9½; ix + 404; 1933.

This book is one of two planned to succeed Bailey's "Cultivated Evergreens;" a second volume on the broad-leaved evergreens will follow later. The pine family and the taxads are treated in considerable detail taxonomically (about 1000 species and varieties are included, many of them illustrated by drawings or excellent photographs), and the recommendations of a number of horticulturists on the selection and planting of the various conifers are given, representing practical experience in several regions. The book closes with chapters on the insects and fungi that attack the conifers. There is a good index.

THE INDIAN FOREST RECORDS. *The Sutlej Deodar. Its Ecology and Timber Production. Vol. XVII, Part IV.*

By R. Maclagan Gorrie. Government of India Press, Calcutta. Rs. 3–2 or 5s. 6d. 7¼ x 9¾; iii + 140 + 6 plates; 1933 (paper).

An attempt to clarify Himalayan sylviculture through a study of the relationship between the variation in the deodar as a timber producing tree and the plants associated with it. The fact that the deodar grows in climates ranging from the heavy monsoon to the extreme aridity found behind the ranges of the Himalayas, implies a similar wide variation of plants found in association with it. The volume consists chiefly of classification and descriptions of these plants.

WORLD WHEAT CROPS, 1885–1932. *New Series, with Areas and Yields, by Countries. Wheat Studies of the Food Research Institute, Vol. IX, No. 7.*

Food Research Institute, Stanford University, Calif. $1.00. 8½ x 11; 36; 1933 (paper).

In this study are presented statistics of wheat production, acreage and yield per acre for each of 40 countries annually from 1919 to 1932 and for 39 countries from 1885 to 1918. It is found that wheat production has increased more slowly during the last half century than had previously been supposed, and that the greater part of this increase was due to increase of acreage rather than of yield per acre. A bibliography of sources of data is included.

UNTERSUCHUNGEN ÜBER DIE MIKROBIOLOGIE DES WALDBODENS. *Erste Untersuchungsreihe. Die elementaren Lebenserscheinungen der Mikroflora und Mikrofauna des Waldbodens.*

By D. Fehér, with articles by R. Bokor and L. Varga. Julius Springer, Berlin. 24 marks (paper). $6\frac{7}{8}$ x 10; vi + 272; 1933.

This is an extensive report on the microbial flora and fauna of the forests of Hungary and of the rôles they play in the nutritional physiology of the forests. It is principally concerned with the researches of Professor Fehér and his associates and includes not only studies on the distribution and identification of the bacteria, fungi, algae, and protozoa of the soil, but also the treatment of the chemical modifications of the soil they induce.

PRINCIPLES OF PLANT PHYSIOLOGY. *Revised Edition.*

By Oran Raber. The Macmillan Co., New York. $3.00. $5\frac{1}{2}$ x $8\frac{1}{2}$; xv + 432; 1933.

The second edition of this textbook for elementary classes has been expanded somewhat by the discussion of recent research. The sections on the chemical aspects of plant physiology are the best ones.

MORPHOLOGY

AN INTRODUCTION TO THE VERTEBRATES.

By Leverett A. Adams. John Wiley and Sons, New York. $3.50 net. $5\frac{7}{8}$ x 9; v + 414; 1933.

This introduction to vertebrate anatomy is intended for beginners in zoölogy and includes résumés at the end of each chapter, a glossary that defines even the commoner technical terms, and a large number of illustrations, many of them original. It is arranged to provide an outline of the characteristics on which the modern system of classification of the chordates is based, a general view of each of the five classes, fishes, amphibians, reptiles, birds, and mammals, and a comparative analysis of anatomical systems and specialized structures, the latter subject taking up most of the book. The text is smoothly and concisely written and the book is provided with a good index.

PHYSIOLOGY AND PATHOLOGY

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome IX: Système Nerveux (Première Partie).*

By Th. Alajouanine, I. Bertrand, Léon Binet, G. Bohn, H. Cardot, L. Cornil, E. Couvreur, P. Gley, H. Laugier, R. Legendre, J. Lévy-Valensi, J. Lhermitte, M. Nicloux, Ch. Richet Fils, J. Verne. Published under the direction of G.-H. Roger and Léon Binet. Masson et Cie, Paris. 80 francs (paper); 100 francs (cloth). $6\frac{5}{8}$ x $9\frac{3}{4}$; xi + 566; 1933.

The first of two volumes on the nervous system appearing in this great French handbook of human physiology. As is the case in other volumes of the series which have been reviewed in these pages the chapters are by various authors. This volume treats of the neurone, Wallerian degeneration and restoration, the processes of nervous disintegration, nerves and reflexes, tropisms, sensibility and motor faculty, cerebral-cortical localizations, the physiology of central ganglia, cerebral circulation, convulsions, sleep, and anesthesia, biochemically considered. Each chapter is equipped with a bibliography.

DISEASES OF OLD AGE.

By F. Martin Lipscomb. William Wood & Co., Baltimore. $4.50. $4\frac{3}{4}$ x $7\frac{1}{4}$; vii + 472; 1933.

An account of the more important facts about illnesses of the aged. The book is designed for clinical use entirely and treats of etiology and pathology only slightly. Although practically any disease can occur in old age, the author has included only those diseases which have a high incidence in old age or those which, although characteristic of maturity, may be conspicuously altered when they occur in the senile.

CANCER: *Is the Dog the Cause?*

By Samuel W. Cort. John Bale, Sons and Danielsson, London. 3s. 6d. net. $4\frac{7}{8}$ x $7\frac{1}{8}$; viii + 190; 1933.

Mr. Cort's argument,' succinctly put, seems to be as follows: Cancer must have a cause; the dog is a filthy animal; therefore, the dog is the cause of cancer. This is not a form of syllogism known either to Aristotle or to any later logician. [I protest! My researches show that 557/632nds of all uplifters reason precisely in this manner. *Reginald. Office Boy.*] [This protest raises an interesting question: Are uplifters logicians? *Platy. Office Fish.*]

THE PHYSIOLOGICAL EFFECTS OF RADIANT ENERGY.

By Henry Laurens. Chemical Catalog Co., New York. $6.00. 6 x 9; 610; 1933.

A useful source book for the practitioner as well as the experimentalist. The author reviews in detail the more outstanding evidences of the physiological action of radiant energy. He emphasizes the great possibilities of helio- and phototherapy, the lack of knowledge at present of the real mode of action of radiant energy and its component parts, the dangers of immoderate use of radiant energy, particularly on the sick individual, and the importance of considering temperature and humidity in treatment. It is shown that, in many divisions the results of radiant experiments are either contradictory or inconclusive. The work contains numerous figures, tables and graphs, a lengthy bibliography and an author and subject index. The volume forms part of the *American Chemical Society Series of Scientific and Technologic Monographs.*

DAS INDIVIDUALISIEREN UND DIE ÜBERWINDUNG DES INDIVIDUELLEN IN DER KRANKENBEHANDLUNG. *Ärztliche Beobachtungen, Erkenntnisse und Wegweisungen.*

By Hermann Königer. Georg Thieme, Leipzig. 1.80 marks. $6\frac{1}{2}$ x $8\frac{3}{8}$; 58; 1933 (paper).

In this little brochure, addressed directly to practitioners of medicine, the author develops the thesis that in the successful treatment of patients the personal idiosyncrasies of each individual must be studied and carefully evaluated. Due consideration must be given to a vast multiplicity of highly variable factors of which the more important relate to bodily habitus, state of nutrition, physiological fluctuations, psychic characteristics, emotional reactions, and the variations of the course of disease processes. Obviously no attempt can be made to give detailed directions for the treatment of patients presenting the multiple combinations of these variables.

LEÇONS SUR L'ALIMENTATION. *Physiologie. Régimes.*

By Giovanni Lorenzini. Masson et Cie, Paris. 36 francs. $6\frac{1}{2}$ x 10; 325; 1933 (paper).

A biochemical and physiological study of metabolism and diet which should be useful to the dietitian and clinician. Following a general discussion of the metabolism of water, minerals, carbohydrates, proteins, fats and lipoids, the factor of age is treated. Diets are also prescribed for persons suffering from disorders of the various organ systems. The book lacks both index and bibliography.

GIANTS AND DWARFS. *A Study of the Anterior Lobe of the Hypophysis.*

By Palmer H. Futcher. Harvard University Press, Cambridge. $1.25. $4\frac{7}{8}$ x $7\frac{3}{4}$; 80; 1933.

This creditable little essay, an undergraduate honors thesis in science from Harvard University, is essentially a short history of the discovery and development of the endocrinology of the anterior pituitary. There is a modest and well selected bibliography of 97 titles.

BIOCHEMISTRY

THE MODE OF ACTION OF DRUGS ON CELLS. *By A. J. Clark. The Williams & Wilkins Co., Baltimore.* $6.25. 5¼ x 8½; vii + 298; 1933.

The Professor of Materia Medica in the University of Edinburgh has put on record his attempt to "try to discover what laws can be postulated regarding the combinations formed between drugs and cells," limiting himself to "picking out cases in which the evidence available seems most complete and trying to find if the phenomena can be explained by the application of the laws of physical chemistry" without making highly improbable assumptions. Clark is not content to catalogue the assumptions that experimenters make, as so many compilers of textbooks do; his guide in such matters is the stern William of Occam, and he has numerous and pertinent criticisms to make of a good deal of recent work in a number of fields of physiology and experimental pharmacology. He takes a healthy interest in figures also:

> In the case of acetyl choline acting on a heart-cell, the relative sizes of the cell and the molecule are as 10^{12} is to one. This is about the relation between a large whale and a small midge. The problem is to form some picture of cell structure that will explain the fact that a few thousand of these molecules when they unite with the cell suffice to modify its functions.

His concern is primarily with the experimental work of the last ten or twenty years and his book cannot fail to have a wholesome effect on all the biological sciences; that is to say, if the people doing experimental work will read it. There are indices and chapter bibliographies.

LIPOIDE UND IONEN. *Eine allgemein biologische und ärztliche Studie über die physiologische Bedeutung der Zell-Lipoide.*

By Rudolf Degkwitz. Theodor Steinkopff, Dresden. 28 marks (paper); 29.20 marks (cloth). 6 x 8¾; xvi + 323; 1933.

The author aims to present for the use of biologists and physicians (1) a summary of the action of lipoids and ions in models, cells, organs and mammals, with a minimum use of chemical, physical and mathematical discussions, and (2) a picture of the structural powers of these substances, and of the knowledge and problems of researches in biochemistry of their form and structure. The usefulness of this handbook is enhanced by author and subject indices, and bibliographic annotations.

CHEMISCHE GRUNDLAGEN DER LEBENSVORGÄNGE. *Eine Einführung in biologische Lehrbücher.*

By Carl Oppenheimer. Georg Thieme, Leipzig. 22.50 marks (paper); 24.50 marks (cloth). 6¾ x 9¾; vii + 298; 1933.

This survey is meant to supplement the various specialized textbooks on physiology and biochemistry in such a way that a medical student or a botanist or a chemist or an animal physiologist could survey the whole field of biochemistry with the aid of the standard texts. The subject matter is limited for the most part to the newer developments and to some of the problems that lie on the boundaries of the several fields of biology. There are an index and a small number of literature references.

MEDIZINISCHE KOLLOIDLEHRE. *Lieferungen 4 and 5.*

Edited by L. Lichtwitz, Raph. Ed. Liesegang and Karl Spiro. Theodor Steinkopff, Dresden. 5 marks each. 7⅜ x 10⅜; Lief. 4, pp. 233–304; Lief. 5, pp. 305–384, 1933 (paper).

The first three numbers of this series were noted in this REVIEW on page 235 of the current volume. *Lieferung* 4 begins the discussions of the application of colloid research in medicine, the various organs and systems of the body being treated separately. These two numbers contain the following papers: Skin, by Franz Herrmann; The eye, by F. P. Fischer; Skeletal system, by R. Bucher; Colloid-chemical physiology and pathology of the joints, by C. Häbler; and Teeth, by Wolfgang Praeger.

ANNUAL REVIEW OF BIOCHEMISTRY. *Volume II.*

Edited by James M. Luck. Stanford University Press, Stanford University, Calif. $5.00. 6 x 8¾; vii + 564; 1933.

This is the second volume of a collection of brief, critical reviews of the progress made during the preceding year or so in each of twenty-five fields of biochemistry. Prominent American and European specialists have prepared the reviews and it is in every way an important and useful book.

THE VITAMINS IN HEALTH AND DISEASE.

By Barnett Sure. The Williams & Wilkins Co., Baltimore. $2.00. 5¼ x 8; xiv + 206; 1933.

The writer has made available to the layman much useful information concerning vitamins, the part they play in health and disease, their presence in foodstuffs, and their effect on milk secretion, infant nutrition, growth, appetite and the teeth. The work is indexed. There is a foreword by Walter H. Eddy.

SEX

THE SCIENCE OF HUMAN REPRODUCTION. *Biological Aspects of Sex.*

By H. M. Parshley. W. W. Norton and Co., New York. $3.50. 5½ x 8½; 319; 1933.

This book of 319 pages, printed on thick paper so that it looks even more substantial, has condensed between its covers a small encyclopedia of the biology of sex, with special reference wherever justified to human reproduction. Logically, chapter II, which sketches the phylogeny of sex, should come first; but "Human Sexual Dimorphism: Man and Woman," which constitutes Chapter I, sounds more attractive, especially to one first fingering the book at a bookstall. The last chapter on the biology of sex behavior likewise allows the book to finish with a bang.

Certain chapters must perforce content themselves with material gathered from studies on animals and plants, as for example, Chapter III on the Sex Cells: cell division, chromosomes, genes, sex chromosomes, gametogenesis, fertilization. It does not take long to say that man has 48 chromosomes and that the XY condition prevails. Chapter IV on the anatomy and physiology of the reproductive organs can be and is written from the human standpoint. The section is much better done than similar parts of many current books on sex.

The following chapter on menstruation, pregnancy, and the life of the embryo is likewise concise and in all essentials correct. It is a brief compendium of gynecology and obstetrics, normal and pathological. One wonders if there is not too much included in the chapter. Chapter VI on sex endocrinology strikes a very modern tone and discloses careful reading and a good digestion of the recent literature. In the limits of a short chapter statements must needs be categorical but one finds no violent misstatements. Chapter VII on sex traits in childhood and adolescence represents the dynamic phase of Chapter I, which is misplaced, as already noted. Perhaps the chapter shows as much as anything the dearth of exact knowledge about physical development in childhood and especially adolescence. In Chapter VIII the author follows Pearl in his conclusions concerning population growth. The author doubts the effectiveness of "positive" eugenics as the savior of the world, but gives arguments for eugenical sterilization. Birth control can hardly be regarded seriously as a "negative" eugenical measure, for "a procedure which involves scientific exactitude and constant foresight is not for the moronic or the feeble-minded."

In the last chapter, the biology of sex behavior, the author does the logical though exceptional thing: he draws upon the more exact observations, meagre as these are, on the sex behavior of lower animals, especially monkeys (Bingham, Zuckerman, Kempf). Some applications to human behavior are well stated and to the point.

The book is "authoritative," as might be expected from the pen of a popular teacher, convincing writer, and sound investigator (mostly in other fields than that dealt with

in this volume). In diction and style the book is far removed from the "popular" class. Its chief use will be in connection with courses in biology in colleges and universities.

SEX DETERMINATION.

By F. A. E. Crew. Methuen and Co., London. 3s. 6d. net. $4\frac{1}{4}$ x $6\frac{3}{4}$; ix + 138; 1933.

In this book Crew presents briefly but adequately the work that has been done on the cytological and genetic aspects of sex-determination.

Sex, in a great many forms, including those with which most of us are acquainted, is determined at the moment of fertilization. The elements of the sex-determining mechanism, brought together by ovum and sperm in fertilization, have been revealed. It is established that in many of these forms, including man, the male is heterogametic, elaborating two kinds of sperm. Any egg elaborated by any female and fertilized by one of these two kinds will yield a male; the same or any other egg fertilized by the other kind will yield a female. In moths, birds and certain fishes, however, it is the female that is heterogametic. The evidence for these statements is presented in this book, being culled from the records of experimental breeding. Sex-linkage, non-disjunction, gynandromorphism, intersexuality and sex-reversal are discussed. The apparently conflicting evidence derived from instances of parthenogenesis is examined, and it is shown that the actual cytogenetical facts relating to parthenogenesis are in accord with those derived from cytological and genetical studies of forms in which sexual reproduction is the rule.

In a final chapter the author speculates on the evolution of the sex-determining mechanism. The value of the book is enhanced by a bibliography of 12 pages, a glossary, and author and subject indices.

KASTRATION INTERSEXUELLER SÄUGETIERE. *Acta Veterinaria Neerlandica, Tome I, Fascicule 1. Edited by Maatschappij voor Diergeneeskunde te Utrecht.*

By G. Krediet. J. van Boekhoven, Utrecht. 5.50 guilders. $6\frac{1}{4}$ x $9\frac{5}{8}$; 120; 1933 (paper).

This is the inaugural number of a series of monographs on veterinary problems and related subjects. The investigations are to be carried on in the European and tropical parts of the Netherlands and the results published in English, French or German. The author of this first number describes castrations he performed on hermaphroditic pigs and goats. His conclusion is that the secondary sexual apparatus is influenced by the gonads, and that the hermaphrodite is not an animal in which male and female attributes exist side by side, the former influenced by the testicular, the latter by the ovarian, cells; but rather that it is an animal which to a certain degree stands *between* male and female and in which the secondary sexual organs and attributes are influenced by a particular kind of gonads *sui generis*. The monograph contains a bibliography of two titles, and several tables of measurements of sex organs of the animals before and after castration.

BIOMETRY

NUMEROLOGY.

By E. T. Bell. The Williams & Wilkins Co., Baltimore. $2.00. $5\frac{1}{4}$ x 8; vii + 187; 1933.

In this diverting book a mathematician at the California Institute of Technology considers the question: Is there more science in numerology than there is numerology in science? As a near neighbor of Hollywood he should be well qualified to judge of the former, while as a resident of Pasadena he should be an equally good judge of the latter. Although he leaves the verdict to the reader, one need not read very deeply between the lines to infer that Dr. Bell considers Eddington and Co. worthy disciples of Pythagoras, both as scientists and as numerologists.

In section 9 of the Appendix there is a neat trap for the unwary reader: "To take an example, is 279 prime? The square root of 279 lies between 16 and 17, since $16^2 = 256$, $17^2 = 289$. So we need try only the primes less than 16, namely 2, 3, 5, 7, 11, 13. A moment's inspection rejects 2, 5 as possible divisors of 279. Try 7; it won't work; neither will 11, 13. Thus 279 is prime."

It will be noted that Dr. Bell has not tried 3 as a divisor of 279. But $279 \div 3 =$

93. Thus 279 is *not* prime. In our experience it is well to watch these mathematicians carefully to make sure that they are not putting something over on us and this caution is especially necessary in dealing with such an impish mathematician as Dr. Bell.

SYMBOLIC LOGIC.

By Clarence I. Lewis and Cooper H. Langford. The Century Co., New York. $5.00. 5¾ x 8¾; xi + 506; 1932.

In the earlier chapters of this book the authors introduce the student to symbolic logic by explaining the algebra developed by Boole and Schröder for use with a logic of classes and its extension to the logic of propositions and propositional functions. As a result of the fact that symbolic logic has in general been built up on a foundation originally designed to deal with the relations of classes, the relation of material implication is much broader than what we ordinarily understand by implication. Thus any two true propositions materially imply each other: "roses are red" implies "sugar is sweet." The authors have built up another system of symbolic logic based on a meaning of "implies" such that "*p* implies *q*" is synonymous with "*q* is deducible from *p*". From this system the customary system of material implication can be derived. Later chapters give the authors' development of the theory of propositions and the application of the logic of propositions to the theory of sets of postulates, while the last chapter deals with logical paradoxes and their bearing on logical theory. There is a bibliography of two pages and an index.

PSYCHOLOGY AND BEHAVIOR

UNIVERSITY OF KANSAS STUDIES IN PSYCHOLOGY *No. 1. Psychological Monographs, Vol. XLIV, No. 1, Whole No. 197.*

Edited by Raymond H. Wheeler. Psychological Review Co., Princeton. $3.75. 6¾ x 9¾; v + 300; 1933 (paper).

The monograph contains in somewhat condensed form the results of thirteen separate studies organized about the general problem of configurational response. Altogether, the papers represent well-directed, thoughtful work in experimental psychology. Heading the list are two papers dealing with cerebral action currents of the dog's cortex. In one, Perkins concerns himself primarily with action currents under sound stimulation, while in the other Bartley maps on the cortex the gradients of electrical activity for a wide variety of stimuli. The latter, rather more emphatically than the other contributors, considers the theoretical implications of recent experimental work and vigorously attacks the concept of specific localization in the cortex. Of considerable interest is his spirited criticism of Pavlov's view of localization, which reads as follows: (p. 47)

> Such a view is sheer atomism. It begs the problem of organization and unity by assuming unity to be a mysterious synthetic product—order coming into existence by summating bits of chaos, a view as archaic as it is absurd. In his attempt to narrow down the conditions of behavior Pavlov has committed the logical fallacy of considering the limited reaction as a discrete process with no relation to the rest of the activity of the animal. The actual situation is that the stimulus-conditions *have been limited*, but, limited or not, an entire organism must respond to the stimuli. Had Pavlov been guided by a field theory instead of by an atomism, much of the ardent labor of the conditioned reflex school would have produced more fruitful and far reaching results. The significance of the "generalized reflex" and of differentiation would have been obvious to him at once, and would have led to an abandonment of the reflex theory of behavior.

Two papers are devoted to the investigation of animal behavior. Margery Cutsforth reports evidence of complex organization or insight in the responses of chicks and Brigden analyses the behavior of white rats that "were unable to choose the correct of three paths to a food goal when the stimulus-pattern was a combination of three vertical lights." Six papers have to do with experimental studies on human beings. Thus Patton, to study insightful behavior, devises a test of relative judgments between pairs of light intensities; Thomas Cutsforth, studying the relation of tactual and visual perception, adds data to support the *Gestalt* conception that the sensory field acts as a functional unit; Brigden finds that "perception involves the differentiation of a homogeneous

[visual] field in such a way that the parts emerge already unified and patterned;" Showalter discusses two aspects of learning, first, the initiation of the learning process by stimulation and, second, the organization of a definite patterned reaction toward which activity takes place; Warden, using five pairs of words for each of the categories, (1) synonyms, (2) antonyms, (3) object-attribute, (4) whole-part, (5) cause-effect, deals with the recall value of the different perceived relations; Sarvis stoutly defends the presence of rhythms in work and learning curves. The maturation of the college student is studied by Baldwin from retests of the National Council tests, and by Roberts from semester grades during the four school years. Finally, Wilcox and Morrison find that the nature of the aesthetic experience varies with intensity of illumination.

PHYLOANALYSIS. *A Study in the Group or Phyletic Method of Behaviour-Analysis.*

By William Galt. Baker and Taylor Co., New York. $1.00. $3\frac{3}{4}$ x 6; 151; 1933.

In this book a student of Trigant Burrow presents the principles and technique of group analysis. The object of these researches is to discover the causes of distortions in the feeling-life of man. In the phyloanalytic group meetings the students are free to express their attitudes towards their associates, attitudes which in every day life are hidden more or less successfully under the veil of courtesy. These attitudes the demonstrator analyzes. As a result of this experimental work it is found "that the prevailing 'normal' social structure is not basic or fundamental in nature but on the contrary represents a secondary and substitutive fabric which, like the fabrications of the neurotic, is without direct biological or organic foundations." Each of us builds up an affectively colored social image of himself. We and those who agree with us must be "right" and "good," while those who disagree with us must be "wrong" and "bad." As a picturesque illustration of this phenomenon in a supposedly normal group Mr. Galt quotes some of the futile bickerings of the United States Senate. The object of phyloanalysis is to make clear this mechanism and thus to bring back the attention from moralistic interpretation to organic reality. We wish that Mr. Galt had stated more specifically how successful the method is in effecting this change of attitude. Certainly a technique which could resolve many of the tensions and irritations of every day life would add enormously to the well being of mankind.

MATERNAL BEHAVIOUR IN THE RAT.

By Bertold P. Wiesner and Norah M. Sheard. Oliver and Boyd, Edinburgh. 12s. 6d. net. $5\frac{5}{8}$ x $8\frac{3}{4}$; xi + 245; 1933.

This book deals "first with a description and analysis of the components of maternal behaviour and then with the results of an examination of the physiological factors related to them." In the study of the components of maternal behavior, which the authors describe in detail, the results are largely in accord with those of previous workers. It was found that maternal behavior could be prolonged by presenting successively young litters to the mother when her own young had outgrown the need of her care. In virgin rats, the retrieving response (one of the definite activities of maternal behavior) was incited in a considerable number when new born young were placed with them. Experiments on destruction of the mammillae, the effects of oöphorectomy and of extracts containing ovarian or gonadotropic hormones are discussed at considerable length. Pronounced maternal activities were observed in a group of animals oöphorectomized and some weeks later injected with extracts. The work includes 23 tables, a bibliography and an index.

THE FIRST TWO YEARS. *A Study of Twenty-Five Babies. Volume II. Intellectual Development.*

By Mary M. Shirley. University of Minnesota Press, Minneapolis. $3.00. $5\frac{1}{4}$ x $7\frac{5}{8}$; xvi + 513; 1933.

This is the second of three volumes which present detailed accounts of the develop-

ment of twenty-five babies observed week by week in their homes from birth until the age of two years. This volume is divided into three parts: Part I describes the course of motor skills, eye coördination, speech, comprehension, and social habits for each baby; Part II gives records of the manner of conducting the observations and taking the records; and Part III "is an attempt to draw all the babies' observed behavior together into an orderly and meaningful whole." Among the conclusions reached is the following:

> Behavior development in infancy always proceeds in harmony with or in conformity to biological laws of development in that: (a) development of behavior follows an orderly sequence that is consistent from baby to baby; (b) there is continuity between human and animal infants in the development of behavior, as is shown by a marked similarity in their developmental sequences; and (c) both human and animal infants adhere to the anatomical laws of developmental direction in that postural and motor control begin headward and travel tailward.

Volume I of the study was reviewed in the QUARTERLY REVIEW OF BIOLOGY, Vol. 7, p. 106.

THE ORGANIZATION OF LEARNING AND OTHER TRAITS IN CHICKENS. *Comparative Psychology Monographs, Vol. 9, No. 4, Serial No. 44.*
By Jack W. Dunlap. Johns Hopkins Press, Baltimore. $1.00. 7¾ x 10; 55; 1933 (paper).

One hundred and nineteen chicks, highly homogeneous as to ancestry, age, vitality and physical environment, were used in these experiments. Ten variables concerned with general nervous activity, spacial relationships, speed in gross muscular activities and directional tendencies, were studied. The means, standard deviations, intercorrelations, reliability coefficients and correlations corrected for attenuation are given. The evidence presented indicates that

> the table of intercorrelations based on ten different tests each on 119 chicks cannot be satisfactorily explained by one general factor plus specific factors. . . . Four factor patterns were fitted to the data, one using eight factors, one using seven factors, one using six factors, and the last using four factors. A general factor pattern using six factors was derived from a consideration of the first three patterns mentioned above and tentative names assigned to the factors.

In two appendices are given notes on *directional tendency* and *fitting factor patterns*. The work includes 26 tables and a bibliography.

THE APE AND THE CHILD. *A Study of Environmental Influence upon Early Behavior. By W. N. Kellogg and L. A. Kellogg. Whittlesey House, McGraw-Hill Book Co., New York.* $3.00. 5¾ x 8¾; xiv + 341; 1933.

In this book is reported a unique study of the infant chimpanzee. On June 26, 1931, Dr. and Mrs. Kellogg "adopted" into their family, as companion and playmate for their 10-months-old son, a female chimpanzee 7½ months of age. During the following 9 months the two infants lived together under *precisely the same environmental conditions* while the Kelloggs observed, recorded and compared the normal and unhampered mental and physical development of their two young charges. Except for the slightly more rapid rate of development of the ape, the two made almost identical progress. In general, the ape surpassed the child only in agility. She learned, for example, to handle a spoon, to drink from a glass, and to open doors more dexterously than the child. Only in respect of imitation and mimicry did the boy clearly show superiority. Without entering "too deeply into the confusing by-paths of the heredity-environment controversy" the authors conservatively conclude; first, "That the heredities of the two are similar enough . . . . to permit similar reactions to the same stimuli," and, second, "That the environment is the activating factor in bringing out the potentialities of the subjects for similar development." Typographically the book is well set up; the illustrations are well chosen; there is a section of references for further reading, and an index.

THE ENERGIES OF MEN. *A Study of the Fundamentals of Dynamic Psychology.*

By William McDougall. Charles Scribner's Sons, New York. $2.00. $4\frac{7}{8}$ x $7\frac{3}{8}$; xii + 395; 1933.

The distinguished author has combined in this book the essential and fundamental theses presented in his two earlier and well known works, *Outline of Psychology* and *Outline of Abnormal Psychology*. This book is an endeavor to present to the student who is just entering the field of psychology a broad outline of the human organism without too much attention to anatomical and neurological details. Such details, the author says, may be postponed until

> The student shall have learnt to conceive and to think about the nature and activity of man in a profitable manner, and, especially, shall have resolutely grappled with the question of the native basis of human personality, its distinguishable factors, their modes of functioning, their growth and differentiation and integration to form the infinitely complex whole.

The author has also added two "novelties." One is a revision of his theory of instincts and intelligence for which he has heretofore been rather sharply criticized, and the other a new treatment of the learning process.

DO YOU SPEAK CHIMPANZEE? *An Introduction to the Study of the Speech of Animals and of Primitive Men.*

By Georg Schwidetzky. E. P. Dutton and Co., New York. $1.75. $4\frac{3}{4}$ x $7\frac{1}{4}$; viii + 133; 1932.

In this interesting but not altogether convincing book Mr. Schwidetzky finds that the sounds made by various animals also occur in human speech and argues that the latter is derived from the former. But a word is not merely a sound; it is a sound which symbolizes a certain meaning. If he could show that the meaning of a word might be derived from the situation in which an animal uses the similar sound his argument would carry greater weight. He also concludes that man resulted from the crossing of widely separated types of primates, such as gibbons and baboons, but gives no evidence that such wide crosses would be possible.

FORTY YEARS OF PSYCHIATRY.

By William A. White. Nervous and Mental Disease Publishing Co., Washington and New York. $3.00. 6 x 9; v + 154; 1933.

An attempt to trace the changes that have taken place in the attitude toward, and treatment of the mentally sick during the last half century. There is a certain amount of autobiographical material interwoven in the narrative but the author has introduced it only as it bears on his views on psychiatry. The book embodies the ripe wisdom of one who has had long and extensive first-hand experience in dealing with the insane.

SELF-CONSCIOUSNESS AND ITS TREATMENT.

By A. A. Roback. Sci-Art Publishers, Cambridge. $1.50 net. $5\frac{3}{8}$ x 8; 122; 1933.

In this little book, written especially for the members of the Society for Adult Education, there is nothing that the average reader cannot easily comprehend. It treats of the symptoms of self-consciousness, the types of people who are self-conscious, the causes and treatment of self-consciousness, etc. etc. A brief bibliography is given and a series of 100 questions by which the reader can test his knowledge of the text. There is an index.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE NEW BACKGROUND OF SCIENCE.

By Sir James Jeans. The Macmillan Co., New York. $2.50. $5\frac{1}{2}$ x 8; viii + 301; 1933.

After the succession of somersaults which it performed in the earlier decades of the twentieth century, theoretical physics seems to have settled down to a comparatively steady state. In this book Jeans sketches the present situation against a background of rudimentary philosophy, "because I believe, in common with most scientific workers, that without a background of this kind we can neither see our new knowledge as a consistent whole, nor

appreciate its significance to the full." He shows how the view of nature as an assemblage of objects external to oneself, located in space and changing with time, arose; and how modern developments in physics have necessitated a new philosophy whose

> essence is that he no longer sees nature as something entirely distinct from himself. Sometimes it is what he himself creates, or selects or abstracts; sometimes it is what he destroys.
>
> In certain of its aspects, which are revealed by the new theory of quanta, nature is something which is destroyed by observation. It is no longer a desert which we explore from the detached position of an aeroplane; we can only explore it by trampling over it, and we raise clouds of dust at every step. Trying to observe the inner workings of an atom is like plucking the wings off a butterfly to see how it flies, or like taking poison to discover the consequences. Each observation destroys the bit of the universe observed, and so supplies knowledge only of a universe which has already become past history.
>
> In certain other aspects, especially its spatio-temporal aspects as revealed by the theory of relativity, nature is like a rainbow. The ancient Hebrew —the analogue of the nineteenth-century physicist— saw the rainbow as an objective structure set in the heavens for all men to behold, the token of a covenant between God and man, and as objective as the signature to a cheque. We now know that the objective rainbow is an illusion. Raindrops break sunlight up into rays of many colours, and the coloured rays which enter any man's eye form the rainbow he sees; but as the rays which enter one man's eyes can never enter those of a second man, no two men can ever see the same rainbow. Each man's rainbow is a selection of his own eyes, a subjective selection from an objective reality which is not a rainbow at all. And it is the same with the nature which each man sees.

As to Heisenberg's celebrated principle of indeterminancy "we can retain *either* the space-time representation of the older pictures *or* the strict determinism, *but never both*." With regard to attempts to press indeterminacy into the service of free-will he is more cautious than some of his confreres. It has always seemed to us that indeterminacy has very little to do with ethics. Moral responsibility depends on the power of conscious choice between alternative acts conceived as good and bad. A person who could act only at random would be as little a free moral agent as one whose acts were mechanically determined. In short the caprices of the electron seem to furnish as poor a basis for free-will as does determinism itself.

THE HEROIC AGE OF SCIENCE. *The Conception, Ideals, and Methods of Science Among the Ancient Greeks. Carnegie Institution of Washington Publication No. 442.*

By William A. Heidel. The Williams & Wilkins Co., Baltimore. $2.50. $5\frac{7}{8}$ x 9; vii + 203; 1933.

The purpose of this book has been "to indicate how the Greeks set about the task of laying the foundations of science, rather than to recount their achievements." It is Heidel's thesis that Greek science differs from modern science mainly in the sense that their methods were the cruder ones adapted to preliminary surveys, and particularly to surveys of a broader scope than are commonly made today. He has arranged his book to illustrate their use of the processes of observation and induction, classification, analogy, and experimentation, and to show that their approach was not different in kind from that of present day science. In particular he is out to controvert the doctrine that the Greeks did not experiment. "The main reason, however, for the infrequency of recorded experiments is the studied brevity of exposition affected by Greek scientists. . . . . Conclusions are offered with only occasional citation of supporting evidence." He has collected a great many of such citations, and we venture to say that almost any scientist ought to find his chapter on experimentation interesting, if not provocative. The book is well documented and has an index.

THE COST OF BIOLOGICAL BOOKS IN 1933

By JOHN R. MINER

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IN ACCORDANCE with the usual custom of the QUARTERLY REVIEW OF BIOLOGY the present paper reports on the cost of books which have been reviewed during 1933. The books are classified as to country of origin in the same rubrics as in previous reports. The prices of foreign books are converted into dollars on the basis of the exchange at the time the books were received.

The total number of pages reviewed in 1933 is 104,725, a decrease of 27.6 per cent from 1932 but an increase of 26.8 per cent over 1926.

As may be seen from Table 2 the general trend of the average prices per page of the biological books reviewed has been downward from 1932 to 1933. Combining all the books reviewed in 1933 the average price per page was 1.005 cents, a decrease of 3.6 per cent from 1932 and of 8.4 per cent from 1926. This is in line with the international decline in general price levels, but, as already noted in the report for 1932, biological books do not seem to have kept pace with other goods in their rate of decline. Thus the books published in the United States show a decrease in price of 8.9 per cent from 1926 to 1933, whereas the wholesale commodity price index of the United States Bureau of Labor Statistics declined about 40 per cent in the same period.

French biological books show an increase in price of 23.3 per cent from 1932 to 1933 and have more than doubled in price since 1926. In all previous years since 1926 French books have been less expensive than any other group of commercially produced scientific books, but in 1933 they are 12 per cent more expensive than English books, which cost less than three-quarters as much as in 1932 and little more than half as much as in 1926. Although the decline in price of English books between 1931 and 1932 probably reflects the drop in the value of the pound during that period, the continued decline in price from 1932 to 1933 cannot be attributed to the same cause, since the pound was stabilized at about 70 per cent of its former value at the beginning of 1932, and varied little in terms of the dollar until the depreciation of the latter in 1933 caused it to rise again. Biological books published in the United States have changed little in price either from 1932 to 1933 or since 1926.

In spite of a decline in price of 10.6 per cent from 1932 to 1933, German books are still the most expensive of any of

TABLE 1

Prices of biological books, 1933

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
German	11,221	$160.15	1.43
British Government	839	11.66	1.39
English-American	9,236	119.45	1.29
United States	59,181	605.80	1.02
Other Countries	2,742	23.41	0.85
France	7,131	52.50	0.74
England	11,426	74.88	0.66
U. S. Government	2,949	4.90	0.17

the groups. The high cost of German medical and scientific publications and especially periodicals bears heavily both on libraries and on individual scientists. A committee of the Medical Library Association, appointed to investigate the situation, found, according to a letter by Eileen R. Cunningham, Chairman of the committee, published in *Science* (Vol. 77, pp. 409–410, 1933), that "in a large or medium-sized library in this country, two thirds or even more of the total annual appropriation for current periodicals is expended on German periodicals, issued chiefly by one or two firms, leaving less than one third of the funds available to be used for the scientific output of all other nations, including the United States and many of the more reasonably priced German publications." The cost of some of these journals has now reached as high as $90.00 to $173.00 a year and, as no definite yearly subscription price is announced, the subscriber cannot know beforehand what he will be called upon to pay. Upon the recommendation of the committee the Medical Library Association has passed the following resolutions (*Science*, Vol. 78, pp. 139–140, 1933):

1. It is recommended that no library subscribe to any periodicals that do not have a fixed annual subscription price for the entire annual output of volumes or parts. That such price be stated in advance, and also a statement of the number and parts to be issued per year.

2. That the Committee on the Cost of Current Medical Periodicals be empowered to invite the various library groups of this and other countries to coöperate with us in the above-mentioned and other measures, necessary to establish more equitable prices for medical and other scientific journals, and that the approach to library organizations in other countries be made first through the president of the International Federation of Library Associations.

3. We believe there is a wide-spread opinion that there must be a substantial reduction in extent of, and in subscription prices for, the most expensive medical and other scientific periodicals, and we further recommend that, unless definite word to this effect is received sufficiently prior to renewal of subscriptions for 1934, libraries cancel their subscriptions to the most expensive journals, except one library in each of 6 to 10 zones throughout the United States and Canada.

TABLE 2

Comparison of the prices of biological books from 1926 to 1933

ORIGIN	AVERAGE PRICE PER PAGE								CHANGE + OR − FROM 1932 TO 1933		CHANGE + OR − FROM 1926 TO 1933	
	1926	1927	1928	1929	1930	1931	1932	1933	Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
English-American	1.55	1.39	1.46	1.90	1.91	2.27	1.48	1.29	−0.19	−12.8	−0.26	−16.8
Other countries	1.51	0.78	1.13*	1.68	0.97	1.53	1.02	0.85	−0.17	−16.7	−0.66	−43.7
England	1.28	1.14	1.09	1.29	1.13	1.19	0.89	0.66	−0.23	−25.8	−0.62	−48.4
United States	1.12	1.09	1.14	1.14	1.09	1.05	1.00	1.02	+0.02	+2.0	−0.10	−8.9
Germany	1.09	1.20	1.48	1.65	1.82	1.75	1.60	1.43	−0.17	−10.6	+0.34	+31.2
British Government		0.96	1.26	0.39	1.19	1.03	1.45	1.39	−0.06	−4.3	+0.43†	+44.8†
France	0.35	0.36	0.45	0.47	0.47	0.69	0.60	0.74	+0.14	+23.3	+0.39	+111.4
U. S. Government	0.31	0.24	0.21	0.23	0.30	0.28	0.36	0.17	−0.19	−52.8	−0.14	−45.2

* With two special treatises omitted as explained in Vol. III, p. 601.

† Change from 1927 to 1933.

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